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SOME OBSERVATIONS ON *PACHYOPHTHALMUS AFRICA* CURRAN (DIPTERA : CALLIPHORIDAE), A PARASITE OF *EUMENES MAXILLOSUS* DE GEER (HYMENOPTERA : EUMENIDAE)

By R. F. Chapman

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Eumenes maxillosus De Geer commonly builds its mud nests in houses, each nest being composed of one or more cells. Each cell initially contains a wasp egg with a supply of paralysed caterpillars to provide food for the grub. The following observations on *Pachyophthalmus africa* Curran, which parasitises the *Eumenes*, were made in the Rukwa Valley, Tanganyika Territory.

Location of Host

Pachyophthalmus africa located the nest of its host by following the wasp as it carried the caterpillars with which each cell was provisioned. Individual flies were seen to sit quite still on walls and furniture for up to eight minutes at a time but sudden movements caused them to turn so as to face the source of the movement, and take-off was induced by any insect flying within about 2 feet. Muscids were frequently seen to elicit take-off but only *Eumenes* was actively followed, otherwise the fly returned to rest. The flies followed the wasps at distances varying between 3 inches and 1 foot, but in ten out of 16 observations they subsequently lost contact with the quarry and returned to rest.

If the fly was successful in following the wasp to its nest it either remained hovering about 4 inches away or landed close by, facing it. So long as the wasp remained at the nest the fly did not approach but as soon as it had left and the nest was empty the fly moved up to it. Flies were only seen to enter nests on three occasions, remaining within for only a few seconds each time.

Two female *Pachyophthalmus*, captured while in pursuit of wasps, were dissected. They contained respectively 40 and 34 eggs which varied in length from 0·6 to 1·0 mm. Larvae emerged from all the eggs, even the smallest, when the chorion was ruptured, suggesting that this species is ovoviviparous. Roubaud (1916) concluded that *Pachyophthalmus pelopoei* (Rondani) was viviparous since he was never able to find the eggs.

Larvae

Newly emerged larvae were found on the outside of the caterpillars in the wasps' cells but they rapidly bored into the body, finally leaving only the dried skin. Although normally the larvae fed on caterpillars they would also eat the wasp grub itself. It appeared that the development of the fly larvae was usually so rapid relative to that of the wasp grub that the latter rarely developed beyond a very early stage. However, partly grown larvae were deprived of caterpillars and given wasp grubs instead. Development proceeded quite

normally. Bequaert (1918) states that *P. pelopoei* fed externally on the caterpillars but did not attack the *Eumenes* grub.

The period of larval development varied from four to eight days, apparently depending partly on the amount of food available, since pupation occurred when the food supply became exhausted. The amount of food available depended on the number and size of the caterpillars in the cell and the number of parasites feeding on them. The number of caterpillars in one cell varied from one to ten (237 counts), the individual caterpillars weighing about 0·2 g. (mean of 38 observations). From one to 31 larvae of *Pachyophthalmus* were found within one cell (54 counts), but over half of the parasitised cells contained five to ten larvae.

The ultimate size of the fly larvae also depended on the amount of food available to them. In the extreme case 24 larvae were found feeding on one caterpillar. Only one of these pupated and the resulting puparium was only 4·7 mm. long and subsequently it failed to hatch. At the other extreme two larvae were found feeding on three caterpillars. The puparia which these larvae formed were 6·5 and 7·4 mm. long.

In some cases there was evidence that the fly larvae had bored from one cell to another within the nest. This was suggested by the presence of small interconnecting holes between the cells, by the presence of obviously eaten caterpillars but no larvae in one cell and sometimes by a very large number of larvae in the second. Thus in single cells only 39 per cent. of those parasitised (54) contained ten or more larvae but with the interconnected cells 86 per cent. contained ten or more (14 observations). This presumably arose from the larvae of one cell being joined by those from another or from a very large initial clutch size.

Such migration from cell to cell appeared to be related to shortage of food. In 54 parasitised cells in which no migration was apparent, only 20 per cent. of the cells contained more than one larva to each caterpillar. Where migration had occurred (14 occasions) there was more than one larva per caterpillar in every case, even after migration had occurred, thereby increasing the number of available caterpillars. The holes between cells were rather less than 2 mm. in diameter, being just large enough to permit the passage of the larvae. Comparable holes leading from the cells to the outside of the nest were never found, suggesting that some stimulus, perhaps olfactory, was directing the larvae.

Puparia

The data on larvae were collected from the examination of completed wasps' nests. These larvae were then put into 3 × 1 inch specimen tubes together with the caterpillars on which they were feeding. When the food was exhausted they readily pupated in dry cotton wool. In those cases where the larvae had already pupated when the cell was examined it was easy to count the number of caterpillars which had provided their food by the number of dried skins.

As already suggested, the size of the puparia varied with the amount of food available to the larvae. For a rough guide it is convenient to regard a caterpillar as a standard unit of food. Then, with one larva per caterpillar the length of the puparium approached 7 mm., decreasing as the number of larvae per caterpillar increased, until at ten per caterpillar the puparia averaged about 5 mm. in length (fig. 1).

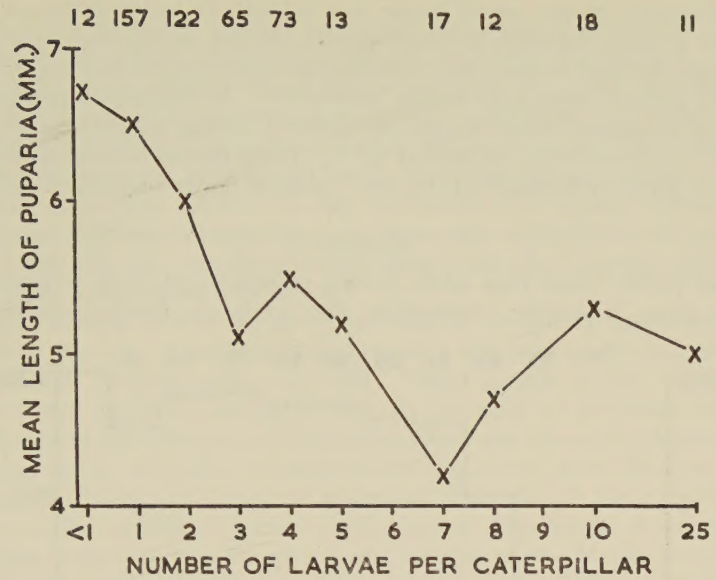

FIG. 1.—The variation in the mean length of puparia depending on the number of fly larvae feeding on each caterpillar. Numbers at the top of this figure and of figure 3 show the number of measurements on which each point is based.

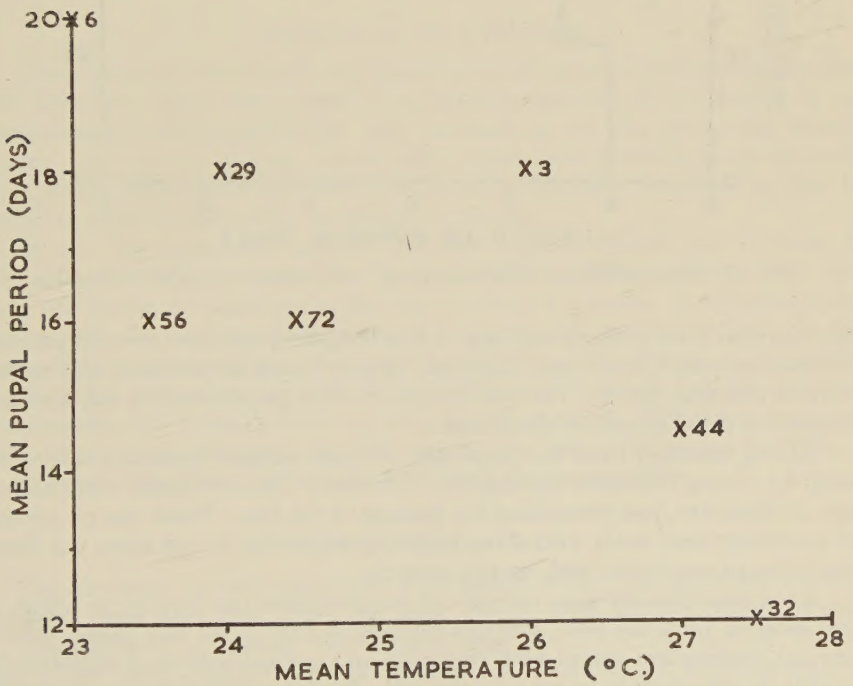

FIG. 2.—Variation in the length of the pupal period according to the temperature to which the puparia were subjected. Figures to the right of each point show the number of puparia used in each observation.

The duration of the pupal instar was related to temperature. Figure 2 shows the average duration for each month plotted against the mean screen temperature for that month, the screen temperature approximating to that at which the puparia were kept in the laboratory. At higher temperatures the duration of the pupal instar was greatly reduced, taking an average of 12 days at 27·5° C. compared with 20 days at 23° C. These figures are comparable with the 15 days given by Roubaud (1916) for *P. pelopoei* under unspecified conditions.

Adults

Ullyett (1950) found that adult *Lucilia* emerged only from puparia above a certain size. A similar observation was made on *Pachyophthalmus*. No

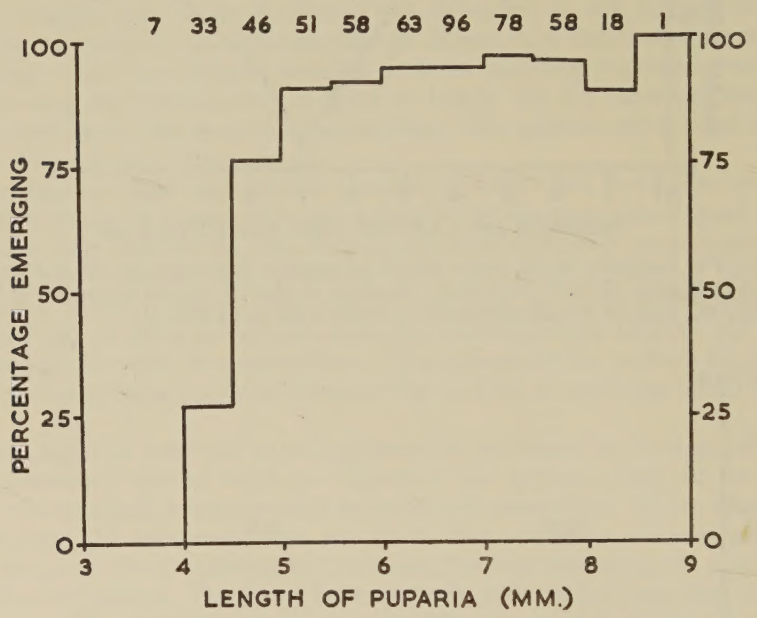

Fig. 3.—The percentage of flies emerging from puparia of different lengths.

flies emerged from puparia less than 4 mm. long and only just over 50 per cent. of those between 4 and 5 mm. hatched. Above 5 mm. 90 per cent. and more of the flies emerged (fig. 3). The vast majority of the puparia which did not hatch showed no development of the imago.

Having emerged from the puparium the flies escaped from the cells of the wasp by boring outwards through the mud wall. The exit holes were about 2 mm. in diameter, just permitting the passage of the flies. There was no question of confusing these holes with those made by migrating larvae since the former were always associated with empty puparia.

A few experiments were carried out to determine the manner in which the flies escaped from the cell. For this purpose a wasp's cell was prised from its original position and sealed with wet mud into a glass-bottomed collecting box so that it was possible to see into the cell. Newly emerged flies were put into it and observations made on their behaviour.

Flies with the wings already expanded and which had started to harden were unable to escape. Softer flies escaped by using the ptilinum. This was inserted into any available crack and alternately expanded and contracted, the whole body of the fly acting as a pump to force fluid into the ptilinum. There was no evidence of any discharge of fluid to soften the earth during this activity and the proboscis was kept folded back. Unfortunately, no really satisfactory method of sealing the cell into the box was found and the flies were always able to force the ptilinum between mud and glass and so break the cell away. The pressure exerted was considerable and escape was effected even when the cell was lightly pressed down with a finger.

Under normal conditions the flies escaped by boring holes in the mud wall. The previous observations suggest that the hole might be produced by the ptilinum, rasping away the wall. Other species of fly, *Voria* sp. for instance, were unable to escape, as was also recorded by Roubaud (1916). This suggested that the ptilinum of *Pachyophthalmus* was specially adapted to assist its escape and to determine whether or not this might be so the armour on the ptilinum of *Pachyophthalmus* was compared with that of the only three other species of fly available at that time, namely *Blaesoxipha binodosa* Curran, *Cordylobia anthropophaga* Blanchard and *Calliphora* sp. It was found that the ptilinal spines of *Pachyophthalmus* were markedly larger than those of *Blaesoxipha* and *Calliphora* and about the same size as those of *Cordylobia*, a much larger fly. This, while being quite inconclusive in the present case, suggests that further study would be of interest.

Degree of Parasitisation

Eumenes nests were found and examined at all times of year except January and February, when the wasps were inactive because of the relatively low temperatures. *Pachyophthalmus* was recorded in all the remaining months except July and its absence during this month was probably only apparent. The period when *Eumenes* was inactive was probably survived by the fly partly as puparia and partly as quiescent imagos.

In all, 234 completed cells of *Eumenes* were examined and of these 90 (38 per cent.) were parasitised by *Pachyophthalmus*. This, however, may have been partly due to collecting within the confines of a house. It is possible that in the open the host would be more difficult for the parasite to find. In this connection it may be significant that in 1955 the observations were made in a new house, only removed from the old by about 100 yards, and the degree of parasitisation by *Pachyophthalmus* was only 22 per cent. (107 nests) compared with 50 per cent. (22 nests) in 1953 and 51 per cent. (105 nests) in 1954. It is, however, impossible to separate this from a seasonal effect.

Other Parasites

The *Eumenes* was also parasitised by a species of Chrysid, and three species of Tachinid were also bred from the cells. These were *Tachina fallax* Meigen, *T.* (*Podotachina*) *sorbillans* Wiedemann and *Voria* sp. Species of *Tachina* and *Voria* have commonly been recorded as parasites of Lepidoptera (*e.g.* Townsend, 1942), and it is probable that they were introduced into the nest by the wasp in already parasitised caterpillars. The same is probably true of some

Braconids, *Cardiochiles* sp. and *Apanteles* sp., which were also found in some cells. In one cell the larva of a beetle, *Mylabris amplecterus* Gent., was found.

Summary

Pachyophthalmus africa Curran is a parasite of *Eumenes maxillosus* De Geer. The fly follows the host to its nest, entering when the wasp departs in search of more food.

The fly is ovoviviparous and the larvae feed on the caterpillars provided by the wasp for the nourishment of its own grub. The larvae take from four to eight days to develop, their ultimate size, and hence that of the puparia, depending on the amount of food available. In the absence of sufficient food they migrate to adjoining cells.

The pupal instar lasts for from 12 to 20 days, depending on the temperature. Puparia under 4 mm. long do not hatch. After emergence the flies escape from the wasp's cell by boring a hole, apparently using the ptilinum for this purpose.

Pachyophthalmus is found at all times of year when *Eumenes* is active, 38 per cent. of the cells examined over the years 1953 to 1955 being parasitised.

Acknowledgments

I am indebted to the late Dr. F. van Emden and Mr. G. E. J. Nixon for identifying the Diptera and Hymenoptera mentioned in this paper.

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FUNCTIONAL AND MORPHOLOGICAL ADAPTATIONS OF THE LARVAL MOUTHPARTS IN THE SUB-FAMILY CULICINAE (DIPTERA) WITH A REVIEW OF SOME RELATED STUDIES BY MONTSCHADSKY.

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Introduction

In this study an attempt has been made to investigate the structural modifications associated with the various feeding habits found in the larval Culicinae. Studies on the structure of the mouthparts have dealt mainly with predatory species (Macgregor (1927), Haddow (1942) and Hopkins (1942)). Beklemishev (1930) and Renn (1941) studied the various methods adopted by larvae for obtaining food, whilst Haddow (1946) recorded the habits of and the effect on other species of some *Eretmapodites* larvae. Hopkins (1952) states " Features of taxonomic interest doubtless occur in the mandibles and maxillae but these have not been studied in African species ". The observations and drawings of the mouthparts in this paper are therefore, as far as is known, all original. Wesenberg Lund (1921), studying Danish culicine larvae, pointed out that there were modifications in their mouthparts and that these were associated with the feeding habits. The only other worker in this field to make any extensive observations was Montschadsky (1936), who dealt mainly with generic differences and concluded that the feeding methods were reflected by the morphology of the mouthparts.

The segmented larvae of the Culicinae are apodous and metapneustic, typically free living and undergo four moults prior to the pupal stage. The pupa is characterised by fundamental morphological changes which include the degeneration of the larval structures and the development of the imago. The larvae are to be found in a wide variety of aquatic environments and the pre-adult life may last from five days to several months. Whilst ground-pools, tree-holes, leaf-axils and domestic water containers will all contain larvae, in a number of cases each species has a well marked breeding site preference. The mouthparts of the larvae are of the generalised type, having well developed mandibles and maxillae and a central mentum composed of the fused segments of a degenerate labium (fig. 1). The typical mode of feeding is by filtering out of the surrounding medium food particles brought by currents set up initially by the pre-oral mouth-brushes. Throughout the various genera specialisations have taken place so that the basic filter-feeding method has given way to browsing and predation, with changes in the mandibles and maxillae, the former becoming larger and more important whilst the latter become smaller. Concurrently with these changes the mouth-brushes have become shorter, stronger and usually serrated.

Functions and Adaptations of the Mouthparts

Whilst variations from the general pattern of action are to be found in the different groups of larvae discussed in this paper, the following description of

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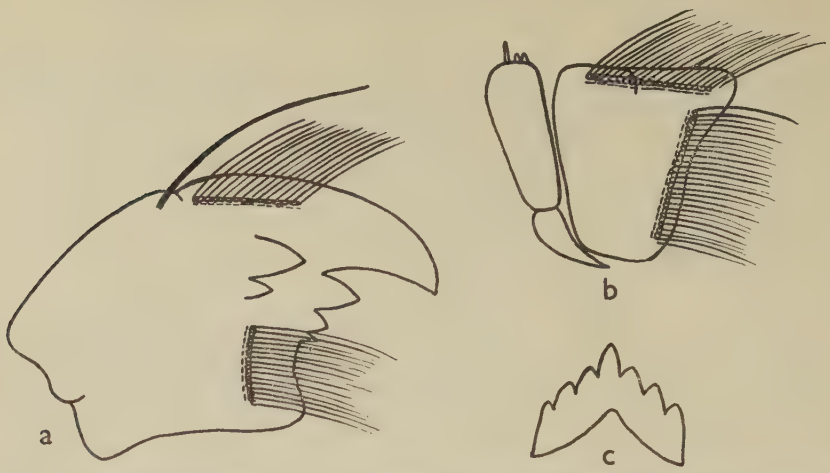

Fig. 1.—Generalised structure of the mouthparts of a Culicine larva: (*a*) mandible; (*b*) maxilla showing two-segmented palpus; (*c*) mentum.

the feeding process has been built up from a series of observations under the microscope. Figure 2 gives the general relationships of the various mouthparts and indicates their main lines of action. The mouth-brushes set up currents in the surrounding water which are directed towards the oral cavity; this corresponds to the "eddy feeding" of Renn (1941). At times the mouth-brushes may become retracted within the oral cavity and help the feeding process by a thrusting motion. Stout setae just inside the labrum have a similar function. The mandibles work over a wide angle in a horizontal plane, the claws manipulating food particles and the setae aiding the general direction of the feeding current. All the movements of the mouthparts may be said to be convulsive, although each part is so co-ordinated that a general peristalsis is set up. The maxillae also have a wide angle of action operating with a thrusting motion towards the mentum, which sits at the oral end of the pharynx. All these movements are accompanied by peristaltic movements of the pharyngeal wall.

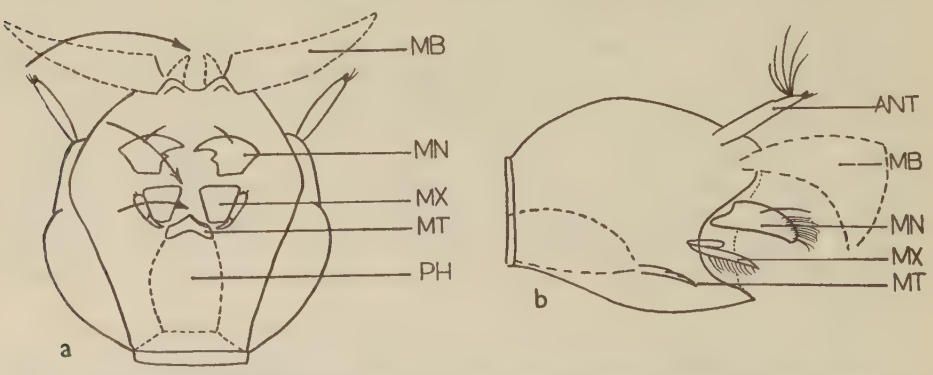

Fig. 2.—Arrangement of the mouthparts with arrows indicating the main lines of action: (*a*) ventral aspect; (*b*) lateral aspect. (*MB*, mouth-brushes; *MN*, mandibles; *MX*, maxillae; *MT*, mentum; *PH*, pharynx; *ANT*, antenna).

The antennae, whilst not primarily considered as part of the feeding apparatus, vibrate during the process of ingestion; this is probably a sensory reaction associated with the search for food, although in the true filter feeders the large sub-apical tufts of setae may well act as an auxiliary straining and current producing mechanism.

Filter Feeders

Filter feeders may be defined as those species which strain out food particles from the surrounding medium, such particles being sufficiently small to pass directly into the digestive tract without undergoing any additional breakdown. The typical filter-feeding facies has been found to be as follows :— long, fine, unserrated mouth-brushes, large maxillae bearing many fine setae, small

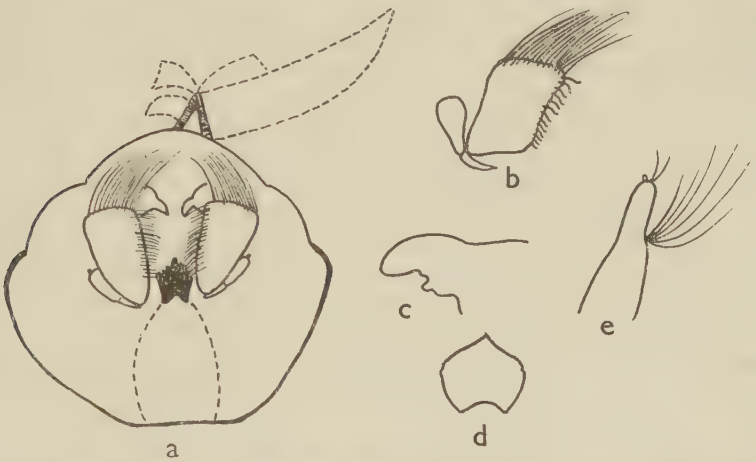

Fig. 3.—(*a*) Mouthparts of *Culex cinerellus*: (*b*) maxilla of *C. argenteopunctatus*; (*c*) mandible of *C. annulioris*; (*d*) mentum of *C. annulioris*; (*e*) sub-apical antennal setae of a typical filter feeder.

weakly chitinised mandibles, a weakly chitinised mentum possessing a large number of very small teeth and, associated with these features, large sub-apical tufts of setae on the antennae. As may be expected, the mouthparts of primary importance in these feeders are the mouth-brushes, which, being long and numerous, are able to set up strong currents over a wide field. These larvae have been observed to hang down from the air-water interface by their siphons so that the mouth-brushes act at about five to ten millimeters below the surface. These morphological and behavioural characteristics are to be found in *Anopheles* larvae, a large number of *Culex* and *Mansonia* larvae and, to a lesser extent, in certain members of the genera *Uranotaenia* and *Hodgesia*, although in the last two there is some tendency to the browsing facies.

The structure of the mouthparts of *Culex cinerellus* Edwards clearly exemplifies this type (fig. 3*a*). The maxillae are approximately two and a half times as long as the mentum, whilst the mandibles are small. The large maxillae and the arrangement of their anterior and lateral setae are typical features, the anterior setae being somewhat longer than the others; the lateral series do not

develop the coarse appearance so typical of the browsing species. In *C. albiventris* Edwards the maxillae have been observed to protrude from the oral region, and their setae, with the mouth-brushes and the antennal setae, form a complex current-producing and filtering mechanism. In both *C. macfiei* Edwards and *C. inconspicuosus* Theobald the lateral setae are very long, extending all the way down the side of the maxillae. In *C. argenteopunctatus* Ventrillon (fig. 3*b*) the lateral series of setae are flagellate in appearance ; this has not been observed in any other related species. It may be that this represents a stage intermediate between filtering and browsing types of setal arrangement. *C. univittatus* (Theobald) and *C. antennatus* Becker, both of which have been taken from ground-pools, have the more typical arrangement of the mouthparts. In the genus *Mansonia* the filter-feeding facies is also to be found. Species of this genus are typically less active as larvae than are the other members of this subfamily. They attach themselves to the stems of water plants, usually *Pistia* spp., by their siphons in order to obtain oxygen and from this position they filter the surrounding water in search of food. It has been observed that the maxillary setae of these species are very abundant. *Theobaldia fraseri* Edwards is another species which shows maxillae typical of this class of feeders, broader than long with very long setae, the anterior series of which may extend beyond the head and mouth-brushes. *Uranotaenia* and *Hodgesia* species tend toward the browsing habit, as indicated by the presence of spines on the maxillae and general shortening of the mouth-brushes, associated with the loss of the sub-apical antennal tufts. These browsing features, as will be seen, are further developed in the genus *Aëdes*.

The mandibles of *Culex cinerellus* are weakly chitinised and have the appearance of rounded hooks. In *C. annulioris* Theobald the mandibles have a weak molar process without any pronounced claw-like area (fig. 3*c*) and in *Mansonia uniformis* Theobald they also appear very small and weakly chitinised. The mentum of *Culex cinerellus*, and all other filter feeders examined, has a large number of small teeth, the extreme case being *C. annulioris* where the edge of the minaret shaped mentum does not bear any distinct teeth but is very finely serrated (fig. 3*d*). The mouth-brushes of the filter feeders which have been examined appeared to be divided into a number of distinct series, most clearly seen in *C. cinerellus*. The major series of brushes, those which were the longest and most numerous, produced the main feeding current, whilst the minor series presumably facilitated the directing of the current and any food particles into the mouth. In *C. thalassius* Theobald it was observed that this major series of brushes was very much shorter than expected, whilst the maxillary setae were stronger than those found in the normal filter feeder ; otherwise the species had the appearance of a typical filter feeder. This combination of characters may bear some relation to the breeding habits of the species, for Hopkins (1952) observed that the larvae have been taken from pools in a mangrove swamp, a canoe, a pool of tidal water, crab-holes, earth drains and a spring. It may therefore be concluded that the peculiar arrangement of mouthparts in this larva contributes to its ability to survive in a wide range of environments. The groups of antennal setae in these species (fig. 3*e*) have already been mentioned, and it has been observed that the antennae accompany the movements of the true mouthparts by sweeping and jerking movements of their own. In *C. perfuscus* Edwards and *C. grahami* Theobald these sub-apical setae are

conspicuously plumose, whilst in *C. macfiei* Edwards, *C. horridus* Edwards and *C. inconspicuosus* Theobald, to cite only three examples, long, very coarse apical setae were observed. Such setae, which were as long as the body of the antenna, would greatly facilitate the process of ingestion. This use of the antennae in these species must be considered as a secondary function as they are pre-oral, innervated from the deutocerebral lobes of the brain and do not resemble the appendages of the post oral somites in either their segmentation or musculature.

Browsers

Browsing in Culicine larvae may be defined as the process of abrasion of solid material, the particles of which require further manipulation by the mouthparts before entering the digestive tract. This process of browsing has been particularly studied in the course of these investigations in the larvae of *Aëdes apicoargenteus* Theobald, *Aë. aegypti* L., and *Eretmapodites chrysogaster* Graham. It was observed that such browsing larvae were typically bottom dwellers, swimming over the substratum or any large submerged objects, at the same time abrading the surface with a combined action of serrated mouth-brushes and mandibular claws and setae. The swimming position usually adopted is at an angle of about 45° to the substratum. Any large particles would be manipulated by the mandibles, whilst the mentum would be used as a secondary grasping organ, foreshadowing its more extensive use in this way in the predators. In a few filter feeders examined some indications of browsing characteristics were observed, mainly in the development of shorter mouth-brushes and coarser maxillary setae, together with the loss of the sub-apical antennal setae. In the genus *Culex*, two species which are usually found in larval environments rich in decaying vegetable matter are *C. nebulosus* Theobald and *C. cinereus* Theobald, both browsing species. These retain some of the filter-feeding characters in combination with others which are typically part of the browsing facies. The mouth-brushes are short but not serrated and the sub-apical antennal tufts are lost, whilst the mandibles possess a row of strong setae. The maxillae are still relatively large but the palpus is small. *Aëdes longipalpis* Grünberg has the browsing characteristics more strongly developed and tends more to the typical facies of this class of feeders. These larvae are found in tree-holes and the nature of these sites and the microbiotic content of the water suggest that browsing larvae would be found in them. The mouth-brushes are still long and unserrated but there is a minor series proximal to the mouth consisting of shorter, stronger setae and the mouth hairs are generally coarser than those found in any filter feeders. The mentum is strongly chitinised and has pointed teeth, whilst the mandibles are also well chitinised and, although still relatively small, have well developed claws. The maxillae are still large but have strong setae. These features are further developed in *Aë. africanus* Theobald, where the maxillae are reduced in size and have strong setae and the mouth-brushes are all short. Similarly, in *Aë. albopictus* Skuse the mouth-brushes are short and distally toothed, whilst in *Aë. ingrami* Edwards the lateral maxillary setae have the appearance of spines without being heavily chitinised. The typical browsing facies are found in *Aë. apicoargenteus* Theobald where the antennae are short and stout, with no sub-apical tuft of setae, the mouth-brushes short and distally serrated, the mandibles strong, with well defined groups of coarse

setae and the maxillae are reduced in size and bear well developed setae (fig. 4*a*, *b*, *c*). This tendency of the mandibles to have strong setae arranged in groups is further emphasised in *Aë. simpsoni* Theobald (fig. 4*d*). Here, although the actual claws are weak, the setae and spines are strong and a mandible of this type is ideally suited to browsing. *Aë. vittatus* Bigot, the larvae of which are found in rock pools, is adapted both for filtering and browsing, the mouth-brushes being long but with serrated tips, whilst the mandibles are small and the maxillae large but armed with strong setae.

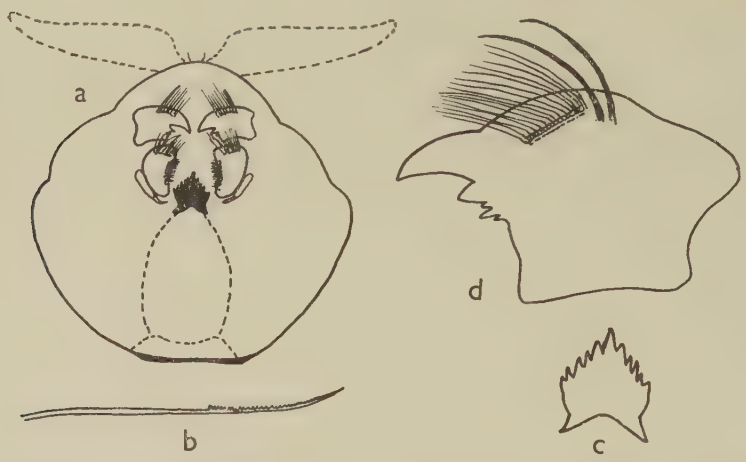

Fig. 4.—(*a*) Mouthparts of *Aëdes apicoargenteus*; (*b*) serrated mouth-brush of *Aë. apicoargenteus*; (*c*) mentum of *Aë. apicoargenteus*; (*d*) mandible of *Aë. simpsoni*.

Predators

Predators are those larvae which attack and feed upon other larvae, typically belonging to other species but sometimes younger instars of their own species, and it has been noticed that they are usually few in number in each breeding site. The predatory Culicine larvae are represented by the genera *Toxorhynchites* and *Eretmapodites*, the *Culex* and *Aëdes* sub-genera *Mucidus* and *Lutzia* and the *Sabethes* and *Psorophora* groups of mosquitoes. In these predatory larvae the role of the maxillae has been further suppressed and the mandibles have become the mouthparts of major importance. The mouth-brushes are usually strongly chitinised and scissor-like in form but in *Culex tigripes* Grandpré they are heavily serrated (*cf.* fig. 5*b*) and the mandibles are the main prehensile organs. The typical predatory facies can be seen in *Toxorhynchites brevipalpis* Theobald (fig. 5*a*). The number of mouth-brushes has been reduced concurrently with their increase in strength and they are gathered into one series only, features which facilitate their prehensile and raptorial function. The mandibles are very large with strongly chitinised claws and take up most of the oral region of the head capsule. Associated with the strong claws are large, stiff spines which also aid in grasping the prey. The development and arrangement of these setae differs from species to species; in *Culex tigripes* the setal group posterior to the main claw is the major one, whilst in *Eretmapodites chrysogaster* Graham the group anterior to this claw is more important. The mentum in all

the predatory species is well developed, the teeth being large and generally pointed. The increase in the strength of the mentum is associated with a reduction in the number of teeth, as is the case with the mouth-brushes. The maxillae in all these species are reduced in size but have strong setae. The palpi are typically small and strongly built, a feature which aids their protection.

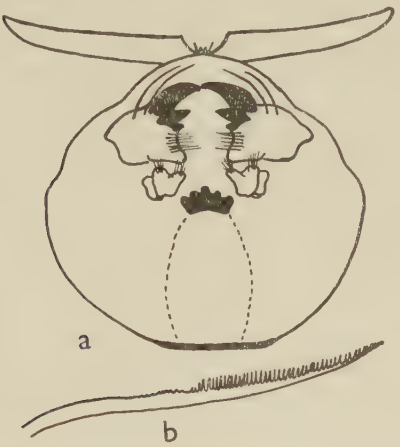

Fig. 5.—(*a*) Mouthparts of *Toxorhynchites brevipalpis* ; (*b*) serrated mouth-brush of *Eretmapodites chrysogaster.*

Discussion

In this study three basic types of feeding method have been discussed, filter-feeding, browsing and predation. This arbitrary classification has been applied here to the Culicinae, but Montschadsky in his work embraced all the genera of the family Culicidae, arriving at a two-fold division : vegetarians and predators. The former category he further sub-divided as follows :—

(*a*) *Surface feeders* : e.g. *Anopheles* spp., *Dixa* spp.

(*b*) *Substratum feeders* : those species which feed below the water surface on various films of micro-organisms and detritus, either on the substratum or on large fragments resting thereon, e.g. *Theobaldia* spp., *Ochlerotatus* spp.

(*c*) *Plankton feeders* : those species which hang from the air/water interface and feed off suspended particles, e.g. *Culex* spp., *Aëdes* spp.

This classification is weakened by the fact that the different feeding classes are based on generic groups only, without any detailed specific studies which would have indicated further differences. The main divergence between this classification and the one adopted here is that Montschadsky places together what have here been called filter feeders and browsers, the *Aëdes* species, as has been pointed out, typically being bottom feeders. His substratum feeders would more closely correspond to the browsers of this present study and, furthermore, the initial dichotomy is inclined to be too broad, as some of the non-predatory species may well be scavengers. The present detailed investigation at specific level shows that a series of species could be arranged, commencing with the true filter feeders and ending with the predators, and including representatives of almost every transitional stage between the extreme types.

Such a gradual increase in specialisation of feeding habit in a series of species or larger group of animals is not peculiar to the Insecta, for in the Crustacea the simpler forms are filter feeders, exhibiting little limb differentiation, whilst prehensile and predaceous appendages are developed in higher members. Thus this proposed series of Culicine larvae would indicate a progression from a generalised method of feeding to a more specialised one, with its associated morphological changes in the mouthparts, as indicated primarily by the suppression of the maxillae and the development of the mandibles. A similar series of changes was demonstrated by Wesenberg Lund in his Danish studies. These trends have been demonstrated in this paper and examples have been given of the various stages to be observed in the Culicinae and, whilst Montschadsky did not trace such a detailed course of events, his observations on the morphological changes are worth discussing at this point.

He pointed out that the labrum, which has not been discussed in great detail here, is the main organ for pushing the food into the mouth and that in predators it aids in seizing the prey. This organ is divided into three parts, of which the lateral ones bear the mouth-brushes whilst the central portion is armed with stiff hairs, the use of which has been mentioned here. He noted that the mandibles are plate-like and bear three types of appendages, hairs, thorns (" kolleth ") and teeth. He observed that substratum feeders had setae on the inner edge of the mandibles whilst those of the plankton feeders possessed only a fringe of hairs, and concluded that the development and the appendages of the mandibles depend primarily upon feeding type and that the greatest development was to be found in predators. He considered that the mandibles had three main functions :

(*a*) The anterior setae of the mandibles are used for cleaning the mouth-brushes.

(*b*) The setae prevent the food from being washed out of the mouth.

(*c*) The claws push the bolus of food toward the mouth, grinding it up in the process.

He stated that the morphological differences to be found in the maxillae are more pronounced than in the mandibles and that these differences are due to the type of feeding habit ; both these points are demonstrated in this present study. In those larvae with pronounced planktonic feeding he observed that the maxillae are narrow with a bunch of hairs at the tip, whilst the palpus is only slightly developed, and that these organs form between them the pre-oral cavity. It has been noted here that in several feeders of this type the maxillae are relatively well developed, but both studies agree that the maxillae of the predatory species are much reduced. He further states that in the palpi of *Anopheles* spp. there are at the distal extremity two finger-like tactile processes but that in all other species of the Culicidae these are absent ; in all the species studied here, however, these sensory processes have been well developed.

It has been shown in this paper that concurrently with the changes in the mandibles and maxillae in the different feeding classes, the antennae also tend to become shorter and to lose the large sub-apical groups of setae, whilst the mouth-brushes become shorter, stronger and reduced in number. These trends within the sub-family may also be traced to some extent in the individual genera. Among *Culex* larvae the majority are filter feeders, whilst there is a tendency in a few forms to the browsing habit and in the sub-genus *Lutzia*

predation is found. In *Aëdes* larvae the trend is similar, but the commonest type of feeding habit is browsing, whilst the predatory forms are represented by the sub-genus *Mucidus*. Exceptions to this rule are *Aë. dalzieli* Theobald and *Aë. simulans* Newstead and Carter, both of which possess the typical filter-feeding facies. This is of particular interest in the case of *Aë. simulans* which is a tree-hole breeder, a niche usually filled by browsers. This parallel development in several genera leads us to consider two further problems, those of the primitive larval environment and of the evolution of predatory larvae within the sub-family.

The unspecialised filter-feeding method is common to mosquito larvae which are found in the ground pool type of environment. Development in this environment of facies tending to browsing and predation would permit colonisation of other larval habitats such as tree-holes. Here the more specialised features would be further developed and this may indicate that ground pools were the primitive larval environment. This colonisation of new larval habitats would be associated with changes in the behaviour of the adults, in the course of which species would appear which would be pre-adapted to the predatory habit. The tree-hole dwelling larvae of the genus *Aëdes* tend towards the predatory facies by having short mouth-brushes which are often serrated, well developed mandibles and partially reduced maxillae, and it may be postulated that browsers with such features were the precursors of the present predatory species. A further species which may be cited in this argument is *Eretmapodites chrysogaster*, the larva of which is considered to be a predator, but is in fact more of a browser. In West Africa these larvae are to be found in great abundance in decaying cocoa husks, the numbers being such that an unlimited supply of other larvae would be necessary to maintain them. Cannibalism may be considered unlikely because of the tough larval integument, although the very young instars are probably eaten by the later ones. This environment would favour the growth and development of a browsing species, presenting as it does a decaying fibrous container rich in available food material. Thus we have in this species an example of what may be called a predator-browser and we may further postulate a primitive larva which may be termed a browser-predator, forming the link between the browsing and the predatory classes of feeders. Different degrees of browsing will be indicated by the structure of the mouthparts and it would be expected that a tree-hole browser would possess stronger mouthparts than a species which browsed on leaves or similar soft decaying matter. Therefore the primitive browser-predator species which has been suggested as the forerunner of the true predator would possibly be a tree-hole dweller. Montschadsky also postulated that predators arose from the planktonic (browsing) class of feeders. Similarly it may be suggested that a predator which retains certain features of the structure and behaviour of a browser is a more recent species, whilst one such as *Toxorhynchites brevipalpis* is much older. This development would take place at different times in the evolution of the various genera and Montschadsky suggested that *Chaoborus* was the oldest, *Toxorhynchites* spp. and the Sabethes group more recent and *Lutzia* spp. the most recent from the evolutionary point of view, whilst he makes no mention of *Eretmapodites* spp.

It may be concluded that those species which are filter feeders are the more primitive, whilst those which have developed more complex feeding habits and have colonised other environments are the more recent. Similarly, those genera

within which there is a greater variety of feeding habits will have a greater potentiality for colonising new habitats, and so the spread of the existing species and the selecton of new ones will be facilitated, a situation which will be intensified in those species showing sub-specific variations.

Summary

The larvae of the sub-family Culicinae are divided into three classes of feeders, termed filter feeders, browsers and predators ; each of these terms is defined. The filter feeders are characterised by long, fine, unserrated mouth-brushes, large maxillae and weakly chitinised mandibles. The browsers have shorter mouth-brushes, serrated distally, whilst the maxillae are smaller and the mandibles stronger. The predators have a few strong mouth-brushes, strongly chitinised mandibles and reduced maxillae. Series of species are described extending from the filter feeders to the predators.

The work of Montschadsky (1936) is reviewed and discussed in the light of these new observations. Ground pools are discussed as the primitive larval environment and tree-hole dwelling browsers as the precursors of the present predatory species.

Acknowledgments

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NOTES ON THE INSECT FOOD OF THE NILE CROCODILE IN UGANDA

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Introduction

Most of the food of young crocodiles (*Crocodilus niloticus* L.) consists of insects. Of the Uganda specimens less than 1 m. long which have been examined so far (Welman and Worthington, 1943 ; Cott, 1954 ; Corbet, 1959), 80 of the 81 containing recognisable food had been feeding on insects. It appears that about 70–75 per cent. of crocodiles between 1 and 2 m. long feed on insects, and that as they grow larger this proportion falls abruptly as first fishes and then birds and mammals assume greater importance as prey.

From the work quoted above it is clear that in Uganda the insects most often eaten by crocodiles are large water-bugs (Hemiptera-Heteroptera : Belostomatidae and Naucoridae) and dragonflies (Odonata-Anisoptera). Several other kinds of large terrestrial insects, notably Orthoptera and Coleoptera, are eaten by young crocodiles, but seldom in numbers large enough to earn them the status of important prey (Table I).

Table I.—*Occurrence of different orders in stomachs of* 44 *insect-eating crocodiles from Lake Victoria*

Order	Occurrence	Main contents*
Hemiptera .	29	16
Odonata . .	16	2
Coleoptera .	8	2
Orthoptera .	9	.
Hymenoptera .	3	1
Dermaptera .	1	1

* Food-type constituting more than half the volume of food in the stomach.

It has been found that examination of the species of insects eaten, and of their condition, can often provide information on where and when they were caught, and can thereby throw an interesting light on the feeding habits of young crocodiles. This paper deals only with the two groups most important in Uganda, the Hemiptera and Odonata. The remarks therefore apply only to crocodiles in Uganda.

Material

These observations are based principally on a sample of 61 crocodiles from the northern end of Lake Victoria, 44 of which contained insect food (Table I). Full data for these specimens, and also for one other insect-eating crocodile from the Albert Nile, are recorded elsewhere (Corbet, 1959). In addition, I

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have received material for identification from Dr. H. B. Cott. This consisted of remains of Hemiptera and Odonata from the stomachs of 32 crocodiles shot by Dr. Cott in Uganda in 1951 and 1952. The data in Tables I, II and III refer only to my material, but those in Table IV include Dr. Cott's.

Results

Hemiptera

Apart from occasional specimens of Corixidae, Gerridae (*Limnogonus* sp.), Naucoridae (*Macrocoris flavicollis* Sign.) and Ranatridae (*Ranatra* sp.), the family principally represented in crocodile stomachs is the Belostomatidae. In Uganda the members of this family provide by far the most important insect food as regards the frequency of occurrence and the volume of food eaten.

The genus *Sphaerodema* may be conveniently considered separately from the other, larger Belostomatidae. *S. grassei* Poisson appears to be the species most often eaten in Uganda, and samples consist almost entirely of adults.

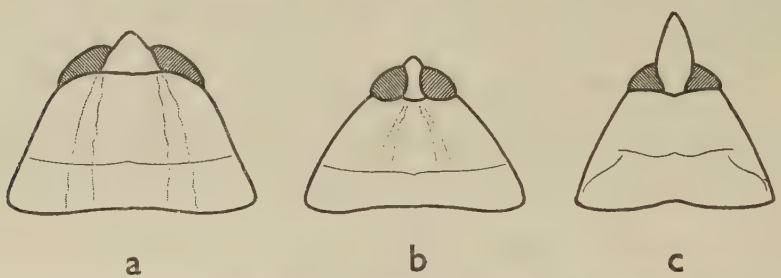

Fig. 1.—Dorsal outline of head and thorax of three Lake Victoria Belostomatidae: (*a*) *Hydrocyrius columbiae* (similar to *H. nanus*); (*b*) *Lethocerus cordofanus*; (*c*) *Limnogeton fieberi*.

All of the 25 specimens retained for identification proved to be this species. Fourteen others (including two larvae) were probably *S. grassei*, as were the 12 adults found in the crocodile from the Albert Nile at Rhino Camp. In my Lake Victoria material, *Sphaerodema* were found only in crocodiles less than 1 m. long, with the single exception of one adult in a specimen 115 cm. long. *S. grassei* is widespread in East Africa, occurring mainly in swamps or slowly-flowing rivers (*see also* Hynes, 1955).

Four species of large Belostomatidae occur in Lake Victoria. One of them, *Hydrocyrius nanus* Montand, is much smaller than the rest. Their approximate lengths are as follows: *Hydrocyrius columbiae* Spin. 58 mm.; *H. nanus* Montand 41 mm.; *Lethocerus cordofanus* (Mayr) 62 mm.; *Limnogeton fieberi* Mayr 52 mm. A fifth species, *Hydrocyrius rectus* Mayr (*ca.* 50 mm. long), has been recorded from Central Africa, but has not been encountered by me in collections from Lake Victoria.

The three larger species can be distinguished by the shape of the head and thorax (fig. 1). All have been collected from marginal grass swamps near Jinja, where they occur commonly and are known to breed. Their occurrence in 44 insect-containing stomachs is recorded in Table II. The presence of breeding individuals may probably be taken as evidence that the

crocodiles were feeding in a swamp. All specimens were adult, except for one large larva of *H. columbiae*.

TABLE II.—*Occurrence of Belostomatidae in* 44 *stomachs*

Species	Number of individuals	Number of stomachs	Number of stomachs with both eggs and adults
H. columbiae . .	25	16	5
L. fieberi . .	20	14	1
Sphaerodema sp. .	39	11	.
Totals . .	84	28*	6

The absence of *L. cordofanus* from stomachs is interesting, since this species is well-represented in mercury-vapour light-trap catches from Jinja, and one might have expected crocodiles to have favoured it on account of its size. None was found in Dr. Cott's material.

Amongst Dr. Cott's material from Lake Bangweulu (Northern Rhodesia) the commonest belostomatid was *Poissonia longifemorata* Brown.

Odonata

The dragonflies eaten by crocodiles consist almost entirely of Anisoptera. The only Uganda record known to me of Zygoptera featuring in stomach contents is provided by one wing found in a crocodile 75–90 cm. long from the Albert Nile at Rhino Camp. Wings of Zygoptera (one being Coenagriidae) occurred in two stomachs from Lake Bangweulu, obtained by Dr. Cott in 1956.

Anisoptera may be eaten as larvae or as adults (Table III). From the point of view of crocodile feeding habits, the aquatic and aerial stages of Odonata should be considered separately.

TABLE III.—*Occurrence of Odonata in* 44 *stomachs*

	Number of stomachs	Number of individuals
Larvae . .	13	24
Adults . .	5	8
Totals .	16*	32

At least nine species of larvae are eaten in Uganda (see Table IV), but the commonest by far is *Ictinogomphus ferox*. During the present work larvae were identified by comparison with reared material, descriptions of five species listed here having already been published (Corbet, 1956, 1957*a*).

The list of species given in Table IV derives from all the material I have examined, *i.e.* 42 stomachs containing Odonata remains. In Table IV the category "*Brachythemis leucosticta*" is expressed thus because during the identification of Dr. Cott's material it is possible that the two species *B. leucosticta* and *Zyxomma flavicans* were confused. Where these species names are given, however, identification was certain. Thus the appropriate figures for these species represent minimum values. From an ecological point of view, this confusion is not serious, since larvae of both species may inhabit similar types of lake shore.

* These totals are not the sum of the individual figures in the column because some of the stomachs contained more than one species of food.—*Ed.*

TABLE IV.—*Occurrence of species of Odonata in 76 insect-eating crocodiles from Uganda*

Species	Larvae		Adults	
	Stomachs	Individuals	Stomachs	Individuals
Ictinogomphus ferox Ramb.	17	33	2	2
" *Brachythemis leucosticta* " (Burm.)	6	6	7	8
Urothemis edwardsi Selys	4	4	2	2
Phyllogomphus orientalis Fraser	2	2	.	.
Sympetrum navasi Lacroix	1	2	.	.
Zyxomma flavicans (Martin)	1	1	2	3
Trithemis annulata (Beauv.)	1	1	3	3
Brachythemis leucosticta (Burm.)	1	1	.	.
Phyllomacromia picta (Selys)	1	1	.	.
Urothemis assignata Selys	1	1	.	.
Anax imperator Leach	.	.	1	1
Orthetrum trinacria Selys	.	.	1	1
Brachythemis sp.	.	.	1	1
Trithemis sp.	1	1	.	.
Gomphidae *indet.*	1	1	.	.
Anisoptera *indet.*	1	1	1	1
Totals	30*	55	20	22

The most important feature of this larval material is that it consists mainly of individuals in the process of emerging, or in an advanced stage of metamorphosis. Diagnosis of metamorphosis is usually unequivocal, and involves examination of the wing-sheaths, eyes and labium. If the wing-sheaths are swollen, or the adult compound eyes are approaching across the mesial line of the head, then metamorphosis is in progress. At this latitude, metamorphosis probably takes about 18 days from the time when enlargement of the eyes can first be discerned. When the adult wing is fully formed inside the larval sheath, and when the tissues of the adult labium have retracted completely within the larval postmentum, emergence will probably occur in 2–4 days ; an individual in such a condition may be termed " pharate " (Hinton, 1946).

It is sometimes difficult to decide whether a fragment of cuticle is derived from a final instar larva, or from an exuvia left behind after emergence. An *I. ferox* larva is often represented only by the terminal abdominal tergites, which appear to be the least digestible parts of the body. (This conclusion is based on the examination of material from fish stomachs). Therefore it seems possible that an emerging adult, eaten with its exuvia, would have long since disappeared by the time that the exuvia had been digested to a stage such that only the terminal abdominal tergites remained.

The 55 larvae found in stomachs were all in the final instar, and of these at least 34 were in an advanced stage of metamorphosis, pharate, or exuviae. Only one of the remaining 21, a *B. leucosticta* larva, was sufficiently well preserved for it to be said that it probably showed *no* sign of metamorphosis. In two instances an exuvia and a newly-emerged adult of the same species were present in the same stomach (*I. ferox* and *Urothemis edwardsi*). The adult *I. ferox* had not yet expanded its wings completely.

* See note on previous page.—*Ed.*

Thus the available evidence indicates that nearly all the prey classified as Odonata larvae was taken at or near the time of emergence. This has interesting spatial and temporal implications. Firstly, it means that the crocodiles have not necessarily been grubbing amongst littoral sand or mud to catch larvae, but have been taking them on, or very near to, the shore. For most of the prey species represented, this would have involved hunting along shores with a firm coast-line; but for *U. assignata*, *U. edwardsi* and *Sympetrum navasi* it would almost certainly have meant hunting along the edge of papyrus swamp. The only species which is characteristic of an exposed, sandy coast line is *Phyllomacromia picta*.

The second fact to be deduced from the predominance of emerging individuals is that the crocodiles must have captured their prey between dusk and dawn, since the normal emergence routine of the dragonflies involved is to leave the water soon after dusk, emerge and dry the wings before midnight, and then to fly at first light of dawn.

The texture of the cuticle and wings, and in certain species the intensity of coloration, can often be used to gauge the approximate maturity of an adult. It is known that newly-emerged dragonflies fly away from water, and return only when sexually mature; thus it may be assumed that whereas an immature adult would have been taken at the emergence site before the maiden flight, a mature adult would probably have been taken over water, or possibly while roosting at night near water.

The species of adults found in stomachs are listed in Table IV. All the specimens of *I. ferox*, *U. edwardsi* and *Trithemis annulata*, and one of "*B. leucosticta*", were definitely immature, and may thus be assumed to have been taken during emergence. By combining records for larvae and immature adults an idea can be obtained of the type of shore along which the young crocodiles were feeding. Thus, of the 42 specimens containing identifiable remains, 34 had obtained their dragonflies from a sheltered shore without swamp, seven from a swamp margin, and one from an exposed shore.

Dragonflies found as unequivocally mature adults in stomachs include *Anax imperator*, "*B. leucosticta*", *Orthetum trinacria* and *Z. flavicans*. (It will be recalled that the records for "*B. leucosticta*" may include or represent *Z. flavicans*.) With the possible exception of *O. trinacria*, these particular species have one important feature in common—a well-defined dusk flight activity over water. This phenomenon in *A. imperator* has been described elsewhere (Corbet, 1957*b*), and is quite distinct from the normal flight activity which occurs during the heat of the day. A similar bimodal flight activity over water has been encountered in *B. leucosticta*. In the case of *Z. flavicans*, a dusk flight only has been observed; this is to be expected in view of the crepuscular and nocturnal habits recorded for the two Malayan species of *Zyxomma* (Lieftinck, 1954). It is interesting to note that *Z. flavicans* was the species most frequently caught mature at mercury-vapour light at Jinja, being taken on 10 out of 100 nights. During the same series of observations, *B. leucosticta* appeared at the trap on three nights, and an unidentified anisopteran, thought to be *O. trinacria*, flew around the trap without being caught on one night at about 35 minutes after sunset.

These observations strongly suggest that small crocodiles (between 90 and 165 cm. long in my records) feed on mature adult dragonflies by catching them

as they fly close to the water at dusk. An observation made at Jinja by Dr. H. B. Cott (*personal communication*) supports this remarkable conclusion : a crocodile lying at the surface of the water was seen to snap at, and apparently catch, a dragonfly passing close to its head.

Acknowledgments

I am very grateful to Dr. H. B. Cott for permission to quote observations on his material, and for reading this manuscript. I also wish to thank Professor R. Poisson for help with the identification of Hemiptera and Dr. W. E. China for permission to examine Hemiptera in the British Museum (Natural History), and for reading the manuscript.

Summary

1. The insects which provide the principal food of crocodiles less than 2 m. long in Uganda consist mainly of Belostomatidae and Naucoridae (Hemiptera-Heteroptera) and of Anisoptera (Odonata).

2. Both in numbers and volume, the Belostomatidae form the most important food of insect-eating crocodiles. In Lake Victoria at least three species of the family are taken, in grass or papyrus swamp, probably at night.

3. Characters are described which enable adults of the larger species of Belostomatidae recorded from Lake Victoria to be distinguished.

4. Most Anisoptera are eaten as they emerge on or near the lake shore at night. Most are obtained from fairly sheltered shores without swamp margins, though a few are caught in swamps, and occasionally also on exposed sandy shores.

5. Young crocodiles also eat mature adult Anisoptera, apparently catching them as they fly over the water at dusk.

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[1] The species referred to here as *P. aethiops* has recently been described by Fraser (1957) under the name *P. orientalis*.

DETERMINATION OF THE AGE OF TSETSE PUPARIA BY DISSECTION

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During work on water balance it was found necessary to determine the age of puparia which were collected in the field and subjected to experimental treatment which caused their death—puparia, that is, whose age could not be established by reference to the date of emergence. The possibility of determining the age of wild puparia by dissection was explored by Potts (1933) but rather broad groupings of pupal stages were used, so that only approximate estimates of age could be made. In an attempt to provide finer discrimination some dissections were made of puparia of *Glossina morsitans* Westw. deposited in the laboratory and maintained at constant temperature. In this way the duration of the different stages could be determined and thus their mean age. It is possible that the results, which are shown in the table, may be of use to workers in other fields.

Table I

Stage	Description	Duration in days	Mean age in days
I	Contents intimately associated with the puparium at all points ; the quiescent phase of the third instar larva	1	1
II	Contents bounded by a fine membrane associated with puparial shell only at rectum ; the fourth instar larva	3	2
III	Imaginal buds evaginated and all adult appendages recognisable ; the pupa *sensu stricto* and pharate adult. This stage can be subdivided on the basis of pigmentation :		
	1. No pigmentation	7	8
	2. Eyes only pigmented		
	(*a*) Eyes yellow	2	12
	(*b*) Eyes reddish-brown . . .	6	16
	3. Eyes pigmented and bristles black . .	3	21
	4. General integument pigmented ; perceptible first on dorsal surface of abdomen		
	(*a*) Pupal skin moist and entire . .	3	24
	(*b*) Pupal skin dry and adhering to puparial shell	2	26
		27	

The puparia dissected had been kept at a temperature of 25·5° C. ; but assuming that the different stages are equally affected by temperature, corrections can be made, using the relation between temperature and pupal period given by Jackson (1949). No distinction was made between males and females,

but even for the longest stage (III, 1) the difference between the sexes would be only a third of a day.

The later stages of pupal development can be determined simply by squeezing the puparium between thumb and forefinger until it breaks, disclosing the pupa. But the early stages (I, II and III, 1) are very fragile and greater care must be taken. An easy method is to imbed the front half of the puparium in a block of paraffin wax, cut it in a ring some distance below the collar of the lobes, and lift off the posterior half.

The duration of stages III, 2a and 2b as given in the table were checked by direct observation of the developing pupae from which a portion of the puparial shell had been removed in the region of the eyes.

Potts (1933) divided the developmental period into four equal parts, each of just under seven days at a temperature of 25·5° C. The first corresponded to I and II of the present scheme, the second to III, 1, the third to III, 2 and the fourth to III, 3 and 4. The agreement is fairly close except that Potts' first stage is four and not seven days, the other three stages being lengthened by equal amounts to make up the deficit.

Fiske's (1920) observation on *G. palpalis* (R-D.), that pharate adults which show pigmentation of the general integument are more than two weeks old, is in agreement with present results.

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A NOTE ON TWO PARASITES OF *PHENACOCCUS INSOLITUS* GREEN (HEMIPTERA : COCCIDAE)

By T. Sankaran

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In the course of work on some Indian Coccids and their natural enemies, the author bred out two species of Encyrtid parasites which have not so far been reported from India, and it is, therefore, considered worth while to record them. Both species were bred from the mealybug *Phenacoccus insolitus* Green, which is a pest of brinjal (*Solanum melongena* L.). Ayyar (1941) mentions that " a predatory lady-bird beetle and a small parasitic wasp have been noted as natural enemies of this mealybug ", but that their exact identity was not known.

One of the species is *Leptomastix nigrocoxalis*, described by Compere in 1928 from male and female specimens bred by E. W. Rust, in Africa, from a species of *Pseudococcus*. Compere writes that the species is somewhat similar to *L. dactylopii* Howard, but that it can be distinguished " by the clear wings, the black coxae of the middle legs, and other minor details of coloration ". The specimens of *L. nigrocoxalis* found parasitising the brinjal mealybug in Banaras emerged mostly from the young and adult females of the host. Some specimens were also bred from male larvae of the mealybug but they generally completed their development and emerged at a time when the host larvae had formed the puparia and were undergoing transformation to the adult stage. Such parasites were stunted in growth and much smaller than those emerging from adult females or from advanced female larvae.

It is interesting to note that *L. dactylopii* has been recorded as a parasite of *Phenacoccus gossypii* Townsend and Cockerell, on *Solanum melongena* in Honolulu, Hawaii (*Notes and Exhibitions*, Meeting of Hawaiian Entomological Society, 12. ii. 1945 (1946, *Proc. Hawaii ent. Soc.* **12** : 464)). *L. phenacocci* Compere, a parasite of *P. hirsutus* Green, was reported to occur in abundance in Cairo, having been introduced into Egypt from Java (Compere, 1939).

The second Encyrtid bred from *P. insolitus* is *Cheiloneurus latiscapus*, described by Compere (1938) from females bred by E. W. Rust from " mealybugs parasitised by *Anagyrus* " in Natal, South Africa. The present author obtained this species from a colony of advanced larval and adult females of the brinjal mealybug parasitised by *L. nigrocoxalis*. Both species of parasite emerged in September, 1950 from hosts collected in the University campus at Banaras. Several species of *Cheiloneurus* are known to have a hyperparasitic relationship with coccids and it is very likely that a similar association may exist between *C. latiscapus* and *L. nigrocoxalis* attacking the brinjal mealybug.

Acknowledgments

The author is grateful to Dr. A. B. Misra for the opportunity of studying in his laboratory some of the coccids and their natural enemies occurring in

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Banaras. Thanks are also due to Dr. B. D. Burks of the U.S. Dept. of Agriculture, Washington, who identified the parasites through the help of Dr. C. F. W. Muesebeck.

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THE LARVA OF *SPILOPSYLLUS CUNICULI* (DALE) (SIPHONAPTERA)

By A. R. Mead-Briggs

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The European rabbit-flea, *Spilopsyllus cuniculi* (Dale), is a common species but surprisingly little was known about its biology before the advent of myxomatosis into Britain in 1953. Interest in this flea was aroused when it was demonstrated to be the principal vector of myxomatosis in this country (Lockley, 1954; Muirhead-Thompson, *unpublished*). Descriptions of some taxonomic characters of the larval *S. cuniculi* are given here and they are compared with those of other described species.

Technique

The material used for this study was obtained from rabbit nests collected in Kent during the spring and early summer of 1957. Several nests were found, each containing one to two thousand larvae. Samples of larvae were taken from these and the rest allowed to develop to the adult stage; these adults were practically all *Spilopsyllus cuniculi*. Only about six individuals of other species of fleas were found amongst the many thousands of adults examined. This method of obtaining larvae directly from nests was necessary as it has been impossible, up to the present, to breed this flea in the laboratory.

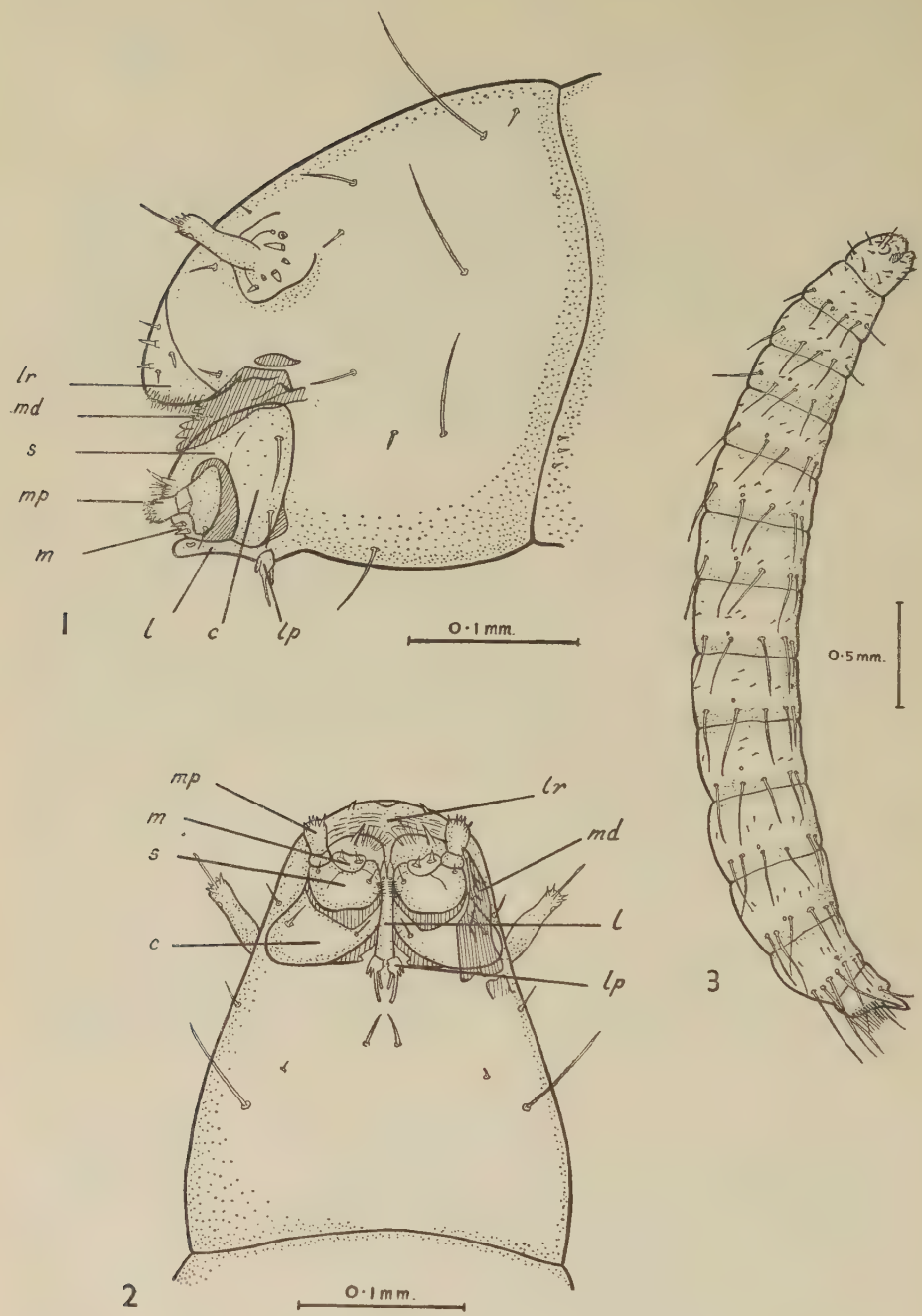
For study the specimens were mounted in Berlese's fluid which cleared them most satisfactorily. In most cases the cover slip was supported by other small slips of glass to prevent distortion of the specimen by crushing. Most of the taxonomic characters described are obvious under low power magnification (×100), but the finer details of the chaetotaxy are best viewed under oil immersion.

Specimens required for measurement were stored in 70 per cent. alcohol after being cleared in 5 per cent. potassium hydroxide solution followed by 10 per cent. acetic acid. The measurements were made with the larvae mounted freely in alcohol in the depression of a cavity slide, so that careful manipulation of the cover slip allowed movement of the larvae into the required orientation.

Description of the Larva

An adequate basis for the description of flea larvae is provided by Sikes (1930). *Spilopsyllus* larvae have the typical form with a distinct head, and a body of 13 segments showing no sharp demarcation from thorax to abdomen.

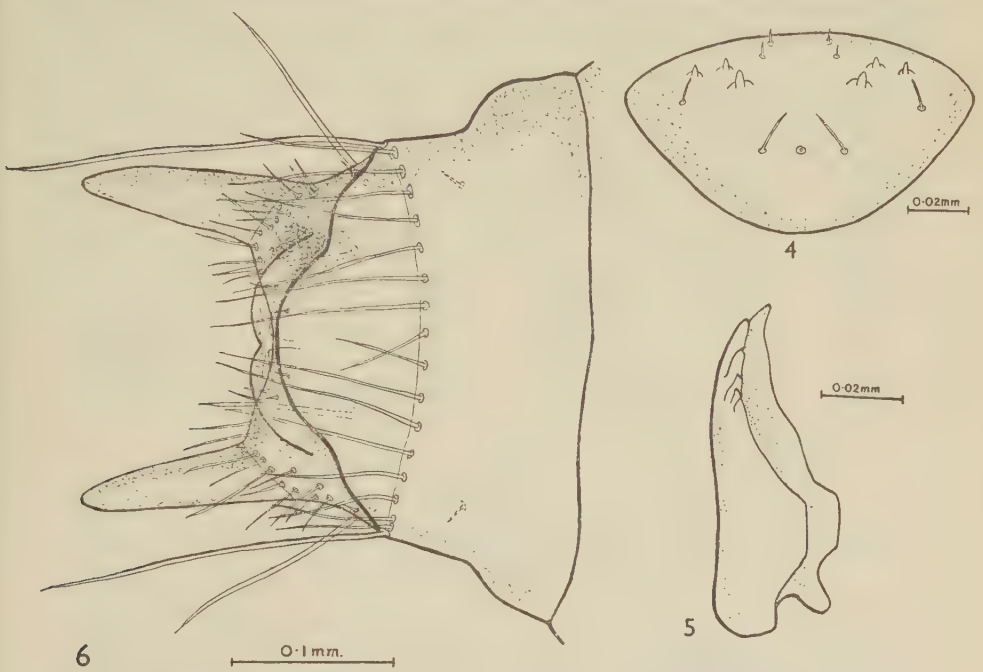
Third instar larva.—The fully grown, but still active, larva is about 4·0 mm. in length. The chaetotaxy of the head is shown in lateral aspect in figure 1, and is similar on the two sides. The setae posterior to the antennae may be grouped into two approximately dorsoventral rows. In the anterior of these there are three long and two short setae. In the posterior row there are three very long setae; one very short seta is situated posterior to the dorsalmost of these. There are two short setae in the frontal region and one



FIGS. 1–3.—*Spilopsyllus cuniculi*, third instar larva. (1) Lateral view of head. (2) Ventral view of head. (3) Lateral view. *c*, cardo; *l*, labium; *lp*, labial palp; *lr*, labrum; *m*, mala; *md*, mandible; *mp*, maxillary palp; *s*, stipes.

on the gena. The labrum (fig. 4) bears two short and two very short setae, and one short and two very short spinous setae on either side of the mid-line. There is a prominent, median sensory pit. Each maxilla (figs. 1 and 2) is divided into a basal part, the cardo (*c*), partly demarcated by thickened chitin from the distal part, the stipes (*s*). The stipes bears a two-jointed palp (*mp*), and a small lobe regarded as a mala (*m*). The labium (*l*) is a long, narrow structure bifurcated distally, and bears typical palps (*lp*). The mandibles (fig. 5) are six-toothed.

Figure 3 illustrates the entire body in lateral aspect. The three thoracic and first nine abdominal segments each bear a transverse ring of long setae



FIGS. 4–6.—*Spilopsyllus cuniculi*, third instar larva. (4) Upper surface of labrum. (5) Dorsal view of left mandible. (6) Dorsal view of terminal abdominal segments, ventral setae seen in transparency indicated by interrupted lines.

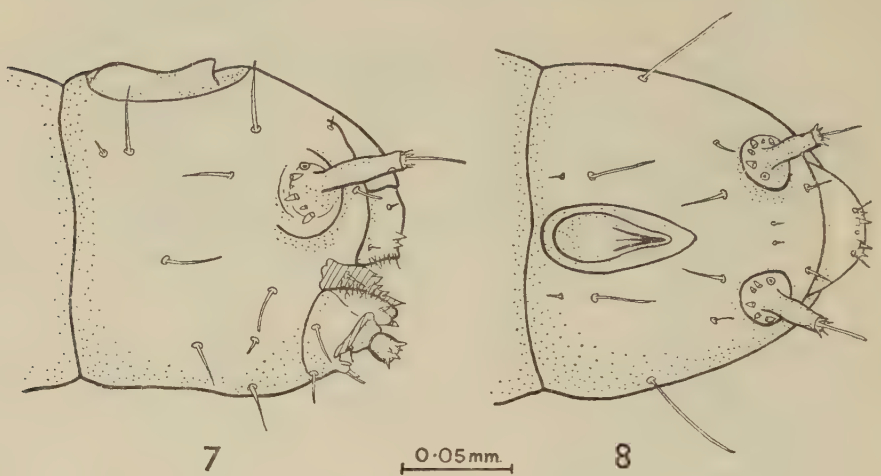
near the posterior border, and another ring of small setae in front of these. The number of pairs of setae on each segment is set out in Table I.

TABLE I.—*The numbers of pairs of setae on the thorax and abdomen of the third instar larva.*

Segment	Anterior row	Posterior row	On dorsal plate
Thorax 1 . .	5 short	5 long	3
„ 2–3 .	5 „	5 „	2
Abdomen 1–6 .	6 „	5 „	1
„ 7–8 .	6 „	6 „	2
„ 9 .	4 „	7 „	3

(There are additionally four pairs of very short setae on the anterior border of the first thoracic segment.)

The chaetotaxy of the tenth abdominal segment shows marked individual variation as in other flea larvae (Bacot and Ridewood, 1914 ; Webster, 1929 ; Elbel, 1952). There is a single, posterior ring of setae, the anal comb, containing on each side seven to nine (normally eight) long, fine setae dorsally and three long, coarser setae ventro-laterally (fig. 6). There is a single short seta anterior to the ventrolaterals. Distally the tenth segment is produced into the anal segment with anal mounds and struts. There are 14 to 17 medium-sized setae (strut setae) near the base of each anal strut. There is often asymmetry in the arrangement of setae in this area ; the numbers noted are 14/16 (as in specimen illustrated in fig. 6), 15/15, 15/16, 16/16 and 15/17.



Figs. 7–8.—*Spilopsyllus cuniculi*, first instar larva. (7) Lateral view of head. (8) Dorsal view of head.

The surface of the cuticle of the body segments is mostly rough, being raised into posteriorly-directed, dentate projections. The areas around the main setae are smoother and known as plates, but these plates are apparently not as distinct in *Spilopsyllus* larvae as they are in most described genera. The numbers of pairs of setae in the posterior ring of each segment which are included on the larger dorsal plate are given in Table I.

The tracheal system is peripneustic and spiracles are present on the first and third thoracic segments, and the first eight abdominal segments. The first thoracic spiracle is on the dorsal plate posterior to, and near the level of, the second seta ; it is keyhole-shaped and clearly open. The third thoracic spiracle is occluded, appearing slit-shaped, and the trachea leading to it is withered. It is not on a cuticular plate, being in the anterior half of the segment between the level of the second and third setae. The abdominal spiracles are all open and approximately pear shaped. The first six are placed just anterior to the second seta of the posterior row, and the seventh and eighth just anterior to the third seta. They are all located on the lateral cuticular plates associated with these setae.

Second instar larva.—The chaetotaxy of the second instar larva appears to be identical with that of the third instar larva.

First instar larva.—The freshly emerged larva is cylindrical and approximately 1·7 mm. in length. The chaetotaxy is similar to that of the second and third instar larvae, and the only obvious difference is the presence of the egg burster on the head (figs. 7 and 8).

Differentiation Between the Three Instars

It is possible to differentiate between the three instars by measurement of the greatest width of the head. Table II shows that in the sample studied there was no overlapping at all between the instars and the differences are highly significant.

Table II.—*The greatest width of the head of larvae of different instars*

Instar	Number measured	Maximum width (μ)	Minimum width (μ)	Mean width (μ)	Standard error
1	10	167	148	156·1	1·74
2	10	189	174	181·3	1·46
3	10	229	215	224·6	1·56

Test of significance :

Instar 1–2 t[18] 11·06 $P \ll 0{\cdot}001$
Instar 2–3 t[18] 20·27 $P \ll 0{\cdot}001$

Note on the Comparative Morphology of Flea Larvae

Although relatively few flea larvae have yet been fully described, those that have include representatives of several families. Table III summarises the characters of a number of these larvae.

There are four subfamilies of the Pulicidae on the British list and, with the present description of the larval *Spilopsyllus cuniculi*, species from each are available for comparison. The larva of *Pulex irritans* L. is more distinct from those of the other described pulicids than the latter are from one another. (The larva of *Echidnophaga gallinacea* (Pulicinae) is described by Elbel (1952) and is atypical of flea larvae generally, lacking one of the usual two rings of setae on the body segments and also having no anal struts). It appears that the larvae of *Xenopsylla*, *Ctenocephalides* and *Spilopsyllus* can only be separated by the chaetotaxy of the head owing to the variability and overlapping of characters on the tenth abdominal segment.

A number of obvious characters separate the larval Pulicidae from the larvae of the Leptopsyllidae and the Ceratophyllidae. The Pulicidae have a single, not a double, row of setae in the anal comb, and the number of strut setae tends to be high. The maxillary palps are Type A, not Type B, of Bacot and Ridewood (1914), *i.e.* the first-joint is short and broad and the second joint long, broad, club-shaped in contrast to a long, broad, cylindrical first joint and a long, narrower, cylindrical second joint. For any one species the chaetotaxy of the seventh and eighth abdominal segments is identical among the Pulicidae, but different among the other families.

TABLE III.—*Summary of the taxonomic characters of the larvae of various fleas*

(L, long seta; S, short seta; T, thoracic segment; A, abdominal segment)

Species	Subfamily	Head: Anterior row	Head: Posterior row	Number of pairs of setae in the posterior rings: T1-3	A1-6	A7	A8	A9	Anal comb: A10	Ventro-lateral	Anal strut	Maxillary palp type	Reference
PULICIDAE													
Pulex irritans	Pulicinae	.	.	5	6	7	7	8	10–12 Single	5	.	A	Bacot and Ridewood (1914)
Xenopsylla cheopis	Xenopsyllinae	3L 1S	3L	5	5	6	6	7	11–13 ,,	3	13+	A	Elbel (1952)
Ctenocephalides canis	Archaeopsyllinae	.	.	5	5	6	6	7	11–12 ,,	3	.	A	Bacot and Ridewood (1914)
Ctenocephalides felis	,,	3L 2S	2L 3S	5	5	6	6	7	9 ,,	3	12	A	Elbel (1951)
Spilopsyllus cuniculi	Spilopsyllinae	3L 2S	3L	5	5	6	6	7	7–9 ,,	3	14–15	A	Present paper
CERATOPHYLLIDAE													
Ceratophyllus gallinae	Ceratophyllinae	.	.	5	6	6	5	6	5–8 and 2–4 Double	3	.	B	Bacot and Ridewood (1914)
Orchopeas howardi	,,	4L 3S	3L	4	6	6	5	6	6 and 4 ,,	3	6	B	Sikes (1930)
Nosopsyllus fasciatus	,,	3L 3S	3L 3S	5	6	6	5	6	8 and 7 ,, 7 and 4	3	8	B	Elbel (1951) Bacot and Ridewood (1914)
LEPTOPSYLLIDAE													
Leptopsylla segnis	Leptopsyllinae	4L 2S	3L 3S	5	6	6	5	6	8 and 1 ,, 6–7 and 3–4	3	7	B	Elbel (1952) Bacot and Ridewood (1914)

Summary

1. The larva of *Spilopsyllus cuniculi* (Dale) is described.

2. Measurement of the greatest width of the head allows the instar to be determined.

3. The morphology of *S. cuniculi* is compared with that of other flea larvae.

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A GYNANDROMORPH OF *TAENIORHYNCHUS* (*MANSONIOIDES*) *UNIFORMIS* (THEOBALD) (DIPTERA : CULICIDAE)

By B. R. Laurence

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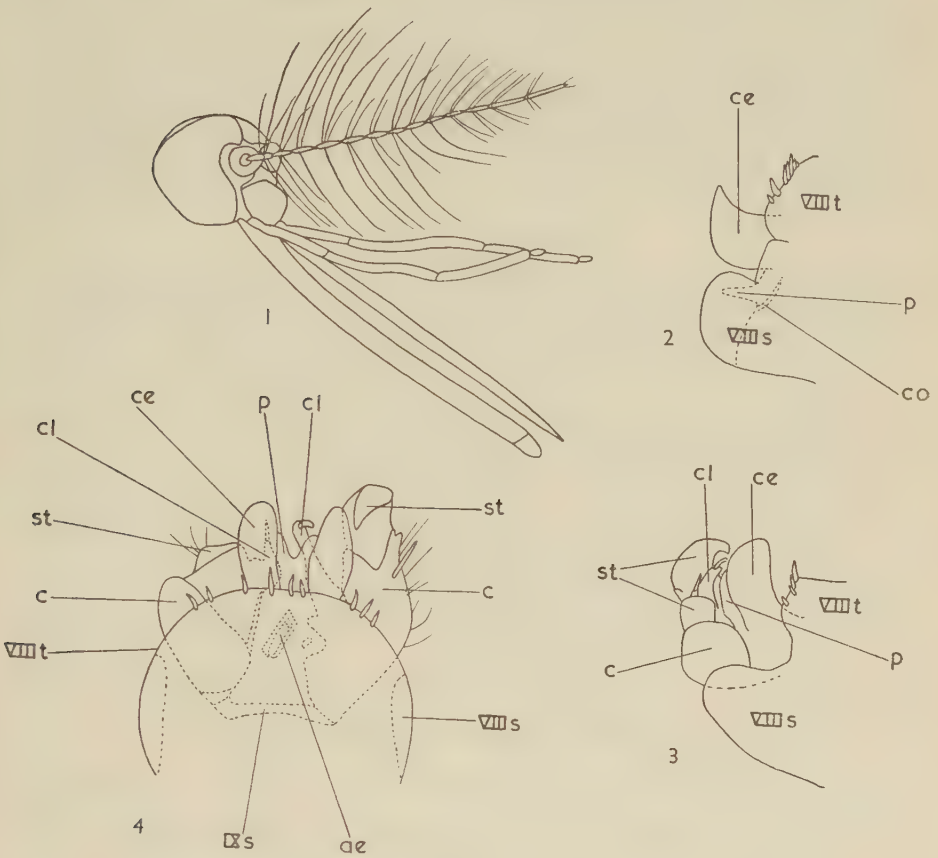
Mosquitoes are reared in entomological laboratories, and captured regularly, throughout the world, yet records of gynandromorph individuals are rare, although Kitzmiller (1953) was able to record descriptions of thirty-four gynandromorphs from six genera—*Aëdes*, *Culex*, *Theobaldia*, *Orthopodomyia*, *Megarhinus* and *Haemagogus*. The rarity of these individuals was shown by Rings (1946), who recorded only four gynandromorphs in an examination of 1,644,050 mosquitoes; and Gilchrist and Haldane (1947) found two gynandromorphs in 9,905 individuals of *Culex molestus* reared in the laboratory at the London School of Hygiene and Tropical Medicine. Gynandromorph individuals have also been reported before in laboratory colonies of *Aëdes* by Smyly (1942). The specimen described below emerged in a colony of *Taeniorhynchus* (*Mansonioides*) *uniformis* (Theobald), originating from Malaya and maintained in the laboratory for two years, and it appears to be the first of its kind to be reported in this genus. The specimen is unusual in the almost symmetrical development of both male and female genitalia. Only one previous mosquito gynandromorph, of *Aëdes punctor* Kirby (v.d. Brelje, 1923), has shown similar symmetrical development of bisexual external genitalia.

Description of gynandromorph specimen (figs. 1–4). General appearance in life of a female. Head with antennae resembling those of male, but the long hairs on each segment of flagellum arising proximally as in female, not distally as in male. Torus of antenna and proportions of segments 1–8 of flagellum as in male. Segments 9–11 of flagellum slightly longer than previous segments (1·4 : 1) (equal in normal male and female); segment 12 twice as long as segments 2–8 (three times as long in normal male, equal in normal female); segment 13 more than twice as long as segments 2–8 (2·8 : 1) (more than three times as long in normal male, slightly longer in normal female). Palps elongate, segmented as in male but only as long as proboscis, rather sinuous and not upturned. Proboscis and mouthparts as in female. Pharynx intermediate in size. Claws on front pair of legs equal as in female, one claw on right leg with basal tooth. Claws on middle legs unequal as in male, but not so large, one claw with basal tooth. Claws on hind legs as in both male and female. Genitalia with cerci and paraprocts as in female (figs. 2–4), but with only one large and one small spermatheca (normally two large and one small), and the eighth tergite with dorsal teeth irregular, and more hairy than in normal female. In the place of the unsclerotised membrane representing the ninth abdominal segment of the female are well developed coxites connected by a rudimentary ninth sternite. Style present on left side but deformed, and right style represented by rudimentary sclerotised plate attached to coxite by membrane. Basal lobes of coxites (claspettes) developed, but deformed on left side, and rudimentary, membranous, on right. Sclerotisation present around genital opening representing aedeagus. Paired ovaries present and no indication of internal male genitalia.

The specimen described above had the appearance of a female mosquito, with the male structures of antennae, palps and genitalia imposed upon it.

Over half the described mosquito gynandromorphs are apparent female mosquitoes with normal genitalia and with the antennae, palps, wings and claws variously modified. More rarely the genitalia are male (Carpenter, 1948; Classey, 1942; Ghelelovitch, 1957; Warren & Hill, 1947), or the gynandromorphs are predominantly male mosquitoes, or bilateral asymmetric mosaics



FIGS. 1–4.—*Taeniorhynchus uniformis* Theobald. (1) Head of gynandromorph; (2) normal female genitalia (lateral view from right side); (3) gynandromorph genitalia (lateral view from right side); (4) gynandromorph genitalia viewed from above, partly through eighth tergite.

ae, aedeagus; *c*, coxite; *ce*, cercus; *cl*, claspette (basal lobe); *co*, cowl; *p*, paraproct; *st*, style; *VIIIt*, eighth tergite; *VIIIs*, eighth sternite; *IXs*, ninth sternite.

(Gilchrist and Haldane, 1947; Marshall, 1938; Muspratt, 1951; Smyly, 1942). Some of the gynandromorphs have attempted to take blood meals (Carpenter, 1948; Edwards, 1917; Smyly, 1942), although Roth and Willis (1952) record specimens of *Aëdes aegypti* L., with female genitalia and with male antennae and palps, responding as males to the vibrations of a tuning fork.

It is difficult to reconcile the predominantly female appearance of the majority of gynandromorphs with the small amount known about sex determination in mosquitoes. Development of male tissue in a female by the loss of one of the X sex chromosomes, which is known in *Drosophila*, does not appear to be possible. Sex chromosomes have not been recognised in the Culicinae, although known in *Anopheles*, and there is no evidence of a sexually inert Y chromosome. According to Gilchrist and Haldane (1947) sex in *Culex* is determined by single genes, maleness (M) being dominant to femaleness (m), and males being M/m and females m/m. These authors supposed that the most probable ways that male and female tissues could be developed from a single nucleus was either by somatic crossing over of M/m, so that some tissue became M/M and some m/m, or by mm going to one pole at a somatic division and MM to the other. Consequently any gynandromorph must begin development with a M/m, or *male*, complement.

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THE INSTARS OF THE WOOD CRICKET *NEMOBIUS SYLVESTRIS* (BOSC)* (ORTHOPTERA : GRYLLIDAE)†

By Peter D. Gabbutt.

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Introduction

As a preface to the study of the bionomics of *Nemobius sylvestris* (Bosc), the immediate problems were to determine and describe the instars and to delimit the generations. The last three nymphs and the life history have been described by Richards (1952) but the earlier instars have not been separated or sexed on a morphological basis.

Materials and Methods

Monthly collections of the insect were made from three sites in Devon over the period February 1953 to May 1955 (details of two of the sites are given in Gabbutt (1956)). At each site 25 random samples, each of area 0·1 sq. m., were taken from the oak leaf litter in a sample area of 250 sq. m.

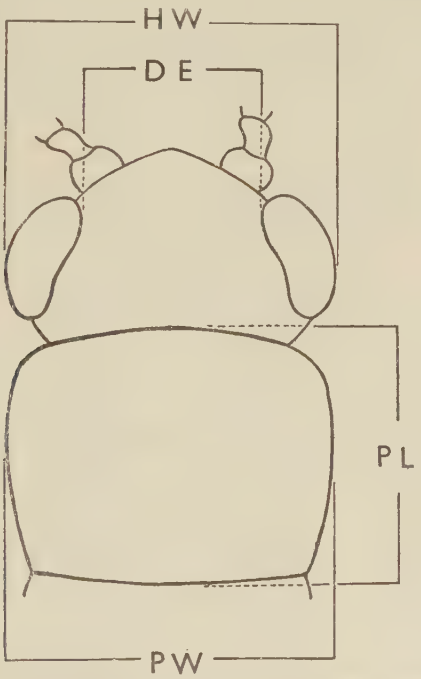


Fig. 1.—*Nemobius sylvestris*. Head and pronotum to show measurements taken. *HW*, head width ; *PL*, pronotal length ; *PW*, pronotal width ; *DE*, distance between eyes. (Setae omitted for clarity.)

* Gabbutt (1953).

† Part of a thesis submitted for the Degree of Ph.D. in the University of London, December 1956.

Each collection contained a number of instars, and younger nymphs were distinguished by measuring the hard exoskeletal parts. Using an eye piece micrometer, with a sliding hair line, the following measurements were obtained from all the individuals irrespective of age (see fig. 1):

(*a*) head width (*HW*);
(*b*) pronotal length (*PL*);
(*c*) pronotal width (*PW*);
(*d*) distance between the eyes (*DE*).

For a particular parameter (*e.g.* head width) the measurements, after grouping, were plotted on arithmetic probability paper and Harding's method (1949) was used to analyse the resulting polymodal distribution.

All four parameters split a particular collection into the same proportions. Table I gives the details of this analysis and shows that the difference between the numbers per size group for each parameter can be accounted for by chance alone (with two exceptions, P is greater than 0·5).

TABLE I.—*Actual numbers per size group as estimated graphically from arithmetic probability paper for the collections made at Harpford Wood, Devon. Four parameters are used; head width* (HW), *length and width of the pronotum* (PL *and* PW *respectively*) *and distance between the eyes* (DE). *Chi-square calculated with respect to the mean.*

		Size Group								
		1	2	3	4	5	6	$\Sigma\chi^2$	n	P
July	HW	108	222	7	.	.	.	0·172	2	>0·9
	PL	108	222	7	.	.	.	0·172	2	>0·9
	PW	101	226	10	.	.	.	1·162	2	>0·5
	DE	101	231	5	.	.	.	0·962	2	>0·5
	Mean	104·5	225·25	7·25	.	.	.	.	.	.
August	HW	.	45	237	126	.	.	0·093	2	>0·95
	PL	.	41	241	126	.	.	0·241	2	>0·8
	PW	.	49	237	122	.	.	0·638	2	>0·7
	DE	.	41	245	122	.	.	0·341	2	>0·8
	Mean	.	44	240	124	.	.	.	.	.
September	HW	.	.	28	179	191	8	4·161	3	>0·2
	PL	.	.	24	183	195	4	0·728	3	>0·8
	PW	.	.	32	191	183	.	5·051	3	>0·1
	*DE	.	.	.	.	.	.	.	.	.
	Mean	.	.	28	184·3	189·7	4	.	.	.
October	HW	.	.	9	35	168	4	0·203	3	>0·95
	PL	.	.	11	41	160	4	0·776	3	>0·8
	PW	.	.	9	35	168	4	0·203	3	>0·95
	*DE	.	.	.	.	.	.	.	.	.
	Mean	.	.	9·5	37	165·3	4	.	.	.
November	HW	.	.	.	11	99	2	0·098	2	>0·95
	PL	.	.	.	10	100	2	0·040	2	>0·98
	PW	.	.	.	10	100	2	0·040	2	>0·98
	DE	.	.	.	10	101	1	0·336	2	>0·8
	Mean	.	.	.	10·25	100	1·75	.	.	.

* Third and fourth instars are not separated using this parameter.

The mean and standard deviation of all parameters for a particular size group was remarkably uniform over successive months. It was assumed that each size group corresponded to an instar, as four different parameters indicated the same trend. To reduce the time spent in examination, only the head width was noted in subsequent measurements.

The mean head width of known first instars, that is those hatching from eggs in the laboratory, did not differ significantly ($t = 1{\cdot}24$) from that of the first size group in the field collections. The latter, therefore, represented the first instar and the results show six instars before the subadult stages described by Richards (1952).

Results

Many collections were made at the three sites and the head width measurements were recorded for all individuals. Later in the study the females of the fifth and sixth instar were recognised but the males of these instars could not be separated on morphological grounds.

The range in the measurements of the head width of a particular instar is shown by subtracting three times the standard deviation from the smallest recorded mean head width and adding a similar amount to the greatest recorded mean head width. The separation of the instars is unsatisfactory because of the overlap in measurements. When the head width is used in conjunction with the number of segments in the antennae, however, most of the individuals can be allotted to an instar (see Table II).

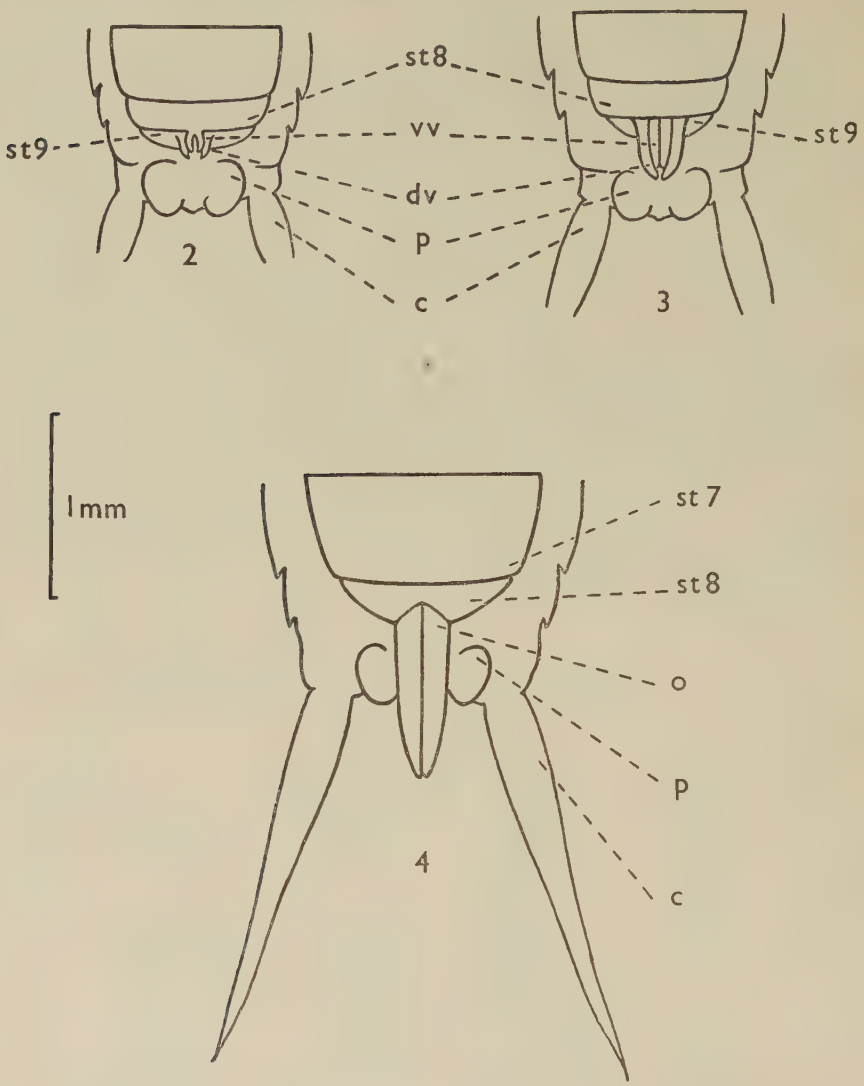
Table II.—*Range in head width measurements for all instars, with the number of antennal segments.*

Instar	Numbers examined	Lowest mean head width in mm.	Highest mean head width in mm.	Range (mm.)	Number of antennal segments.
1	912	0·70±0·03	0·77±0·02	0·61–0·83	31–34 usually 33
2	1174	0·90±0·03	0·93±0·02	0·81–0·99	40–55
3	1143	1·06±0·02	1·11±0·03	1·00–1·20	53–67
4	962	1·22±0·05	1·29±0·01	1·07–1·32	61–78
5♂	217*	1·43±0·03	1·48±0·04	1·34–1·60	72–93
5♀	215*	1·43±0·03	1·49±0·02	1·34–1·55	
6♂	40*	1·61±0·06†	1·64±0·04†	1·43–1·76	86–103
6♀	48*	1·62±0·05†	1·67±0·05†	1·47–1·82	
7♂	185	1·71±0·06	1·88±0·11	1·53–2·21	over 100
7♀	175	1·72±0·05	1·99±0·09	1·57–2·26	,,
8♂	129	2·04±0·06	2·15±0·04	1·86–2·27	,,
8♀	120	2·12±0·05	2·30±0·07	1·97–2·51	,,
Male	419	2·25±0·04	2·38±0·07	2·13–2·59	,,
Female	393	2·46±0·07	2·65±0·07	2·25–2·86	,,

* Numbers low because these instars were not sexed until comparatively late in the study.

† Corrections made for small numbers in the sample.

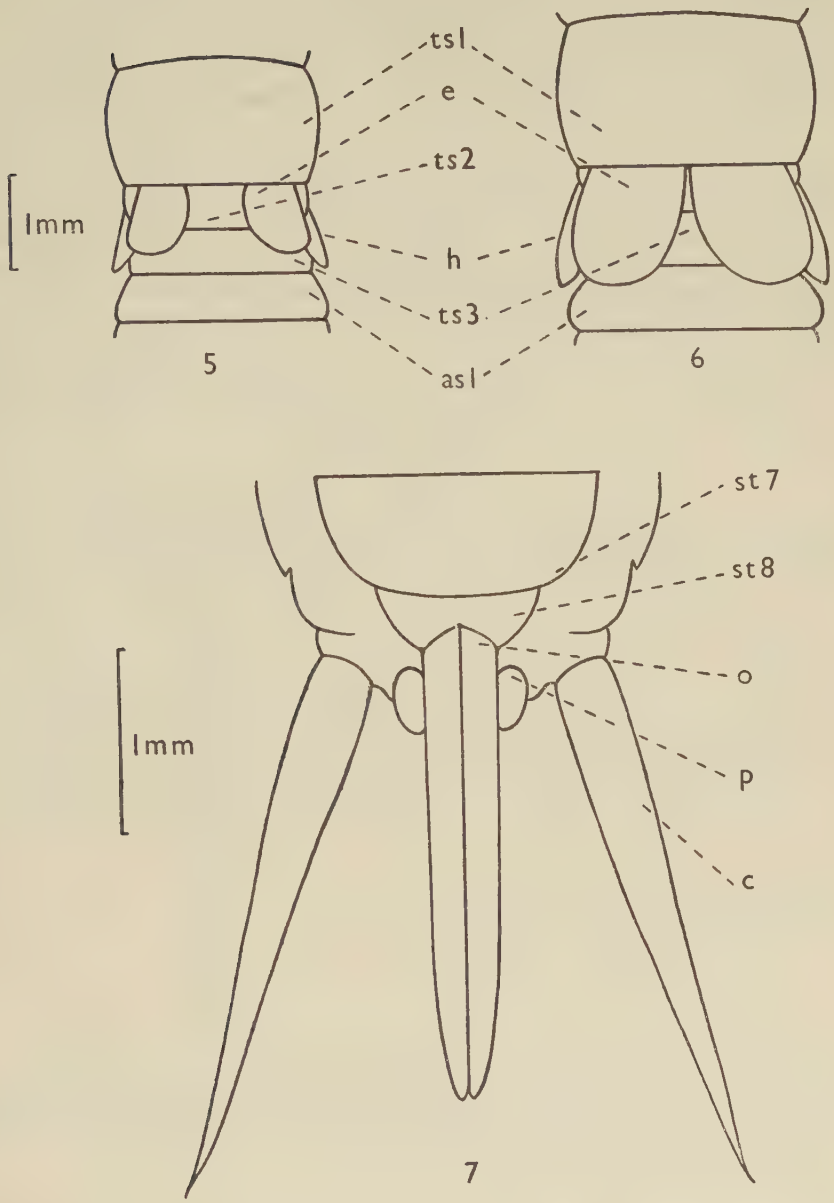
A description of the instars from the fifth onwards is given below. The males have been separated by the form of the elytra; the females by the position and length of the ovipositor.



Figs. 2–4.—*Nemobius sylvestris*. Ventral view of posterior abdominal segments of females: (2) Fifth instar; (3) Sixth instar; (4) Seventh instar. *c*, cercus; *dv*, dorsal valve; *o*, ovipositor; *p*, paraproct; *st* 7–9, sternites 7–9; *vv*, ventral valve. (Setae omitted for clarity.)

Female

Fifth Instar (fig. 2): ventral and dorsal valvulae appear as small tubercles on posterior edges of eighth and ninth abdominal sternites respectively; dorsal valve barely reaches the paraproct.



Figs. 5–7.—*Nemobius sylvestris*. Dorsal view of anterior region of males: (5) Seventh instar; (6) Eighth instar. (7) Ventral view of the posterior abdominal segments of a female: eighth instar. *as* 1, abdominal segment 1; *c*, cercus; *e*, elytron; *h*, hind wing; *o*, ovipositor; *p*, paraproct; *st* 7–8, sternites 7–8; *ts* 1–3, thoracic segments 1–3. (Setae omitted for clarity.)

Sixth Instar (fig. 3): valvulae stouter and longer and project slightly over the paraprocts.

Seventh Instar (fig. 4): half total length of ovipositor extends beyond abdomen and can be seen from dorsal surface (ovipositor total length ≃ 1 mm.).

Eighth Instar (fig. 7): ovipositor nearly as long as cerci; about four-fifths of total length (≃ 3 mm.) can be seen from dorsal surface.

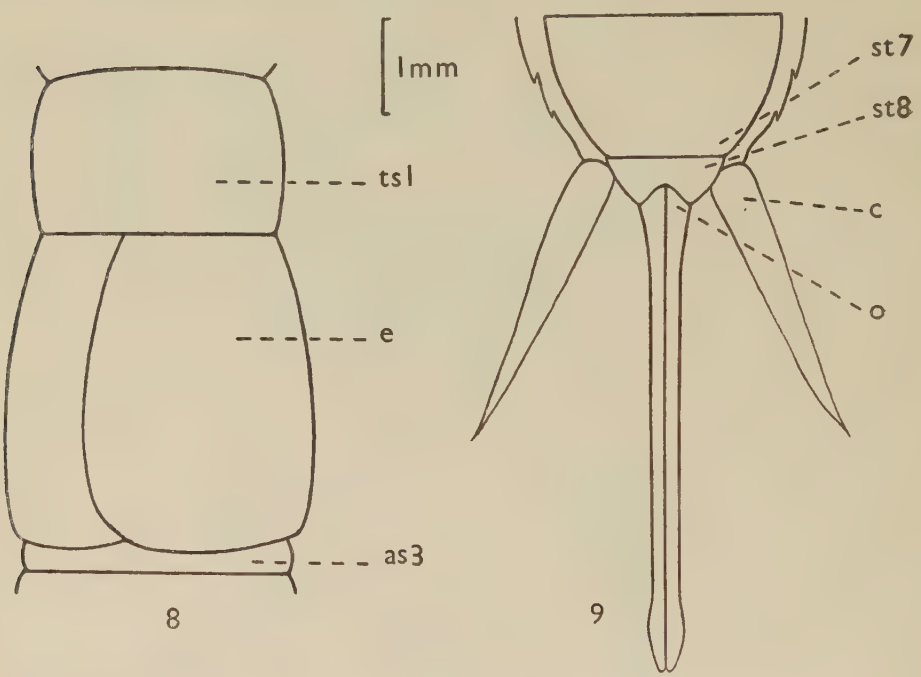
Adult (fig. 9): ovipositor (≃ 5 mm.) almost twice as long as cerci. Elytra present in seventh and eighth instars and in adult.

Male

Fifth Instar: no valvulae visible on ventral side; no sign of elytra on dorsal side, posterior to pronotum. Head width: 1·34–1·60 mm. Antennal segments: 72–93.

Sixth Instar: as for fifth instar. Head width: 1·43–1·76 mm. Antennal segments: 86–103.

Seventh Instar (fig. 5): elytra appear as small outgrowths from second thoracic segment, and are, in part, covered by the pronotum and extend posteriorly to middle of third thoracic segment; hind wings arise from third thoracic segment and are nearly covered by elytra.



Figs. 8–9.—*Nemobius sylvestris*. (8) Dorsal view of anterior region of adult male; (9) Ventral view of the posterior abdominal segments of adult female. *as* 3, abdominal segment 3; *c*, cercus; *e*, elytron (right); *o*, ovipositor; *st* 7–8, sternites 7–8; *ts* 1, thoracic segment 1. (Setae omitted for clarity.)

Eighth Instar (fig. 6): elytra enlarged, meet in the mid-dorsal line and extend posteriorly partly to cover first abdominal segment; elytra overlie the hind wings.

Adult (fig. 8): the great extension of the elytra posteriorly and medially is noticeable; right elytron overlies the left and both extend posteriorly to cover third abdominal segment.

Life History

A detailed analysis of the life history will be published later but the essential details are as follows. The life history is uni-voltine. The eggs are laid during the period August–November and undergo diapause, hatching the following June–July. The adults normally die off at the end of the year but occasional males and females are still to be found in March–April. The first instar is present in June and early July and successive instars until November, when the insect normally over-winters as the fifth or occasionally the sixth instar. Growth recommences the following April and the sixth, seventh and eighth instars are present in the following two months until the adults finally appear in July or early August.

Acknowledgments

I wish to express my gratitude to Professor L. A. Harvey for his help and advice at all stages of this work ; to Mr. M. J. Delany, Mr. I. Linn, Mr. G. G. Vickers and Mr. T. J. Richards for their interest and advice and finally to my wife for help in the preparation of this paper.

Summary

1. The nymphs of *Nemobius sylvestris* (Bosc.) are described.

2. Early instars are separated on the basis of head width measurements, whilst the fifth and later instars can be sexed and separated morphologically.

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BIOLOGICAL EVIDENCE FOR THE SPECIFIC SEPARATION OF *CRYPTOLESTES CAPENSIS* (WALTL) FROM *C. SPARTII* (CURTIS) (COLEOPTERA: CUCUJIDAE)

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Introduction

In a summary of identifications of over 3500 samples of the genus *Cryptolestes* found on stored foods (Howe and Lefkovitch, 1957), *C. spartii* (Curtis) was recognised on 81 occasions. Illustrations of the genitalia of that species were given, analogous with those given by Reid (1942), and Steel and Howe (1952, 1955) for the other species discussed. Howe and Lefkovitch (*op. cit.*) pointed out that two colour forms of *C. spartii* exist, a black form living in the burrows of certain Scolytids on broom, *Sarothamnus scoparius* (L.) Wimmer, and an otherwise identical brown form found on stored foods. They were not certain whether the difference in coloration was due to different feeding habits, microclimatic conditions, etc., or even whether the different colours indicated a specific distinction. The genitalia of the two forms were found to be identical in both sexes. Since the genitalia of other species of *Cryptolestes*, where known, show large differences, the two forms were considered to be conspecific. The brown form has generally been considered to be a variety of *C. spartii*, being the so-called var. *capensis* Waltl, although Grouvelle (1908), in a key to the African species of *Laemophloeus sens. lat.*, considered *capensis* to be specifically distinct from *spartii*.

To discover the nature of the relationship existing between these two colour forms, living material of both was obtained.

Experimental Method

Source of Living Material

(a) *Black form.*—Massee (1952) recorded the presence of *C. spartii* on broom at Dungeness, Kent. He kindly informed me of the precise locality of his finds and the method of capture. With Mr. G. E. Woodroffe of this Laboratory, I collected 19 living black adults of *C. spartii* on 5th–6th June, 1957, together with the insects listed in Table I.

(b) *Brown form.*—This form has been in culture at this Laboratory since 1954. The original stock and subsequent additions to it were obtained by culturing living representatives when these were sent for identification by inspectors of the Infestation Control Divisions of the Department of Agriculture, Scotland, and the Ministry of Agriculture, Fisheries and Food.

TABLE I.—*Insects collected on broom*, Sarothamnus scoparius (*L.*) *Wimmer at Dungeness, Kent, 5th–6th June*, 1957

Coleoptera

Apion immune Kirby
A. striatum Kirby
Curculio nucum L.
Bruchus villosus auctt. (*sens.* Joy)
Dromius notatus Steph.
Dryophilus anobioides Chev.
Hylastinus obscurus (Marsh.)
Isomira murina (L.)
Kateretes rufilabris Latr.
Meligethes spp.
Micrambe vini (Panz.)
Monotoma spinicollis Aubé.
Phloephthorus rhododactylus (Marsh.)
Phytodecta olivacea (Forst.)

Diptera

Calliopum geniculatum (F.) Meig.

Hemiptera

Anthocoris nemoralis (F.)
A. sarothamni Douglas and Scott
Arytaina genistae (Latr.)
Dictyonota strichnocera Fieb.
Heterocordylus tibialis (Hahn)

Psocoptera

Elipsocus westwoodi Mc.

Identifications were carried out by Mr. C. E. Dyte (Diptera), Dr. W. J. Le Quesne (Homoptera), Dr. B. P. Moore (Coleoptera), Mr. G. E. Woodroffe (Coleoptera and Heteroptera) and the author (Coleoptera and Psocoptera).

Laboratory Procedure

The 19 black adults collected at Dungeness were placed on a mixture of rolled oats and wheatfeed in a constant temperature room at 20° C. After three days, three adults were dead. Two days later, the culture was placed at 25° C., 70 per cent. R.H., a set of conditions known to be favourable to the brown form. This culture was left undisturbed for 80 days. On examination it was found to contain 11 larvae. Only five adults were still alive, 11 having died. Each larva was placed in a $2 \times \frac{1}{2}$ inch glass specimen tube containing a small quantity of the wheatfeed/rolled oats mixture (*c.* 100 mg.) and closed with a centrally pierced, muslin-covered cork. After a further 22 days, 20 more larvae were found. Each of these larvae was isolated in a similar manner to those found previously.

Virgin adults of the brown form were obtained by removing large larvae or pupae from a culture and isolating them individually in specimen tubes in the same way as were the larvae of the black form. Some results of observations upon the physical limits of the brown form (to be published later) are given for comparison; they were obtained in exactly the same way as were those for *C. ugandae* Steel and Howe given by Lefkovitch (1957).

Males of both colour forms can be easily recognised since their mandibles possess a large external tooth visible dorsally or ventrally.

RESULTS

Developmental Period

Observations upon the periods required for the development of black *C. spartii* are scanty but there is a marked similarity to the periods required by the brown form (Table II). The prepupal and pupal periods are almost identical and it is likely that their larval periods are of the same order.

TABLE II.—*Developmental periods in days of brown and black "C. spartii" at 25° C., 70 per cent. R.H.*

	Egg	Larva	Prepupa	Pupa	N
Brown .	5	27·9	3·0	7·8	25
Black .	.	At least 28	2·9	7·8	19

Adult Weight

On the day they became adult beetles were weighed on a torsion balance of maximum capacity 1 mg. and with scale divisions of 0·002 mg. Mean weights are given in Table III. These suggest that at 25° C., 70 per cent. R.H., black beetles are heavier than the brown.

TABLE III.—*Weight of adults in mg. on day of emergence when bred at 25° C., 70 per cent. R.H.*

	Males			Females		
	N	Mean	± SE	N	Mean	± SE
Black .	12	0·329	±0·047	13	0·298	±0·045
Brown .	11	0·274	±0·039	7	0·233	±0·027
	P less than 1%			*P* less than 1%		

Adult Colour

Newly adult animals of the black form were brick-red in colour, indistinguishable from the brown form. After two days, the head and pronotum were black, the elytra remaining brick-red. After four days, with the exception of the legs, the whole beetle was black. This is the typical full coloration of this form.

Even the very oldest living brown form adults that have been observed (at least six months as adult) were ferruginous in colour. In no series of this form collected together were there any dark individuals.

Crossing Experiments

Two patterns of procedure were used. The results of the first to be described indicate that the methods used inhibited egg production.

In the first experiment, unmated males and females of both colour forms, less than two days old as adult, were placed in 2 × ½ inch specimen tubes with a little wheatfeed. Five pairs of each combination (*i.e.* male and female of different colour) were set up together with four pairs of each colour as controls. No eggs were obtained after a month from any of the pairs nor were there any signs of egg-eating by the adults.

Using the adults from the inconclusive experiment described above, four small jars were each provided with some wheatfeed, rolled oats, yeast and a tube of dilute glucose solution accessible via a strip of filter paper. In jar A were placed the four black pairs, in B the four brown pairs, in C the five black males and five brown females, and in D the five brown males and five black females. After nine days a black male and brown female were seen copulating. After 35 days cultures C and D were examined for larvae. In both cultures the

females and in D a male were dead and in neither were there any larvae. In cultures A and B, examined on the following day, numerous larvae were found. There had been no deaths amongst the adults. Moreover, isolated and virgin adults were still alive after five months.

The offspring of culture A were black and two further generations have shown no indications of colour change even on an entirely cereal diet.

Discussion

The presence of cross-mating in these two colour forms suggests that there is a close relationship between them, but lack of breeding and the resulting death of the females indicates an effective biological isolation. Similar female deaths as a result of interspecific mating have recently been reported by Park (1957), although its effects were not so immediate in *Tribolium* as they have been in the species forming the subject of this paper.

The developmental periods recorded in Table I are very similar to each other but differ considerably from those of some other species of *Cryptolestes* (Lefkovitch, 1957 ; and unpublished results). In the conditions of the experiments the black form was about 0·05 mg. heavier than the brown form. This weight difference may be unimportant, since in *C. ugandae* it has been shown that the weight of newly formed adults varies considerably with the temperature and humidity at which the larvae have developed (Lefkovitch, 1957). As has been found to be usual in this genus, males were larger and heavier than females.

In spite of the apparently identical genitalia in the two colour forms, the failure of attempts to induce cross-breeding together with the different biological niches and the constant difference in adult colour strongly support the conclusion that there are two distinct species involved. Fortunately, names exist for them, the black species being *C. spartii* (Curtis) (= *ater* Olivier) and the brown species, *C. capensis* (Waltl). Thus Grouvelle (1908) was correct in considering the latter species as distinct from the former, but since he gave no new reasons subsequent authors did not follow him.

It should be noted that all the records given by Howe and Lefkovitch (1957) of *C. spartii* refer to *C. capensis*.

On the evidence so far available it appears that the two species have an almost identical geographical distribution which can be briefly defined as Europe and North Africa. Grouvelle (1908) considered that *C. capensis* was cosmopolitan in its distribution, but Howe and Lefkovitch (1957) were not able to confirm this. Recently, three specimens of this species bearing the data " 1410. Gold Coast. ii. 1942. G. S. Cotterell. On tomato seeds imported from S. Africa " were found in the collection of the Commonwealth Institute of Entomology. In describing the species Waltl (1834) wrote " In einer Art Kleye, die als *Emballage* vom Cape der guten Hoffnung kam, waren ein Menge von Larven, die erzogen einen *Cucujus* lieferten." These two records of the species possibly indicate the presence of *C. capensis* in southern Africa, although the latter record should be treated with caution owing to the possibility of cross-infestation. It would not be surprising if *C. capensis* is established in Southern Africa since there is a similarity between the climatic conditions of that region and of Mediterranean Europe.

Acknowledgments

I should like to acknowledge Dr. Massee's help in giving me precise details of the locality in which he found *C. spartii* and Mr. G. E. Woodroffe's assistance in their collection. I am grateful for the identifications carried out by the gentlemen listed in Table I. Thanks are also due to the Commonwealth Institute of Entomology for allowing me to examine their collection. This work formed part of the research programme of the Pest Infestation Laboratory and is published with the permission of the Department of Scientific and Industrial Research.

Summary

Hitherto, the brown storage form of *Cryptolestes spartii* (Curtis) has been considered to be a variety, *capensis*, of the species which occurs in a black form on broom. Although both forms are otherwise apparently morphologically identical and the black form can be bred entirely upon cereals, cross-mating between virgin adults did not produce fertile eggs and caused the early death of the female. This evidence suggests that the two are specifically distinct, *C. capensis* occurring on stored foods whilst *C. spartii* (*sens. strict.*) occurs on broom.

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CONTRIBUTIONS TO THE STUDY OF THE SEXUAL BEHAVIOUR OF *SCHISTOCERCA GREGARIA* FORSKÅL (ORTHOPTERA : ACRIDIDAE)

By Werner Loher

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I. Introduction

The largest group within the suborder Acridoidea, or shorthorn grasshoppers, is the subfamily Catantopinae with over 2000 species (Beier, 1955). The European fauna, however, has only a few representatives and probably for that reason they have received much less attention than the subfamily Truxalinae (Dirsh, 1956), the sound producing organs of which are very characteristic : the hind femur bears on the inner side a series of pegs which rub against a strongly developed vein of the corresponding fore wing. Such a stridulatory organ is lacking in the Catantopinae. In the latter, Varley (1939) described another form of stridulation in *Oedaleonotus fuscipes* Scud., in which the mandibles rub against each other, making a " gentle clicking sound ", while Faber (1949) found in *Calliptamus italicus* L. no less than half a dozen different mandibular noises and was able to show that they play a role in the sexual behaviour.

The purpose of the present work on the Desert Locust (*Schistocerca gregaria* Forsk.), also a member of the Catantopinae, was to investigate the general sexual behaviour and in particular to find out whether and to what extent acoustical components are involved.

II. Material and Method

The insects investigated came from the laboratory of the Anti-Locust Research Centre. They were kept in a constant temperature room at 28–30° C. The males and females of the gregarious phase were 10–12 weeks of age and had already copulated. Several days before the experiments the individuals were isolated in 2-pound glass jars. The observation cage was 60 cm. high, 60 cm. long and 60 cm. wide ; its four sides were mainly of glass and the ceiling consisted of milkglass, which diffused the light of five 25-watt bulbs ; the bottom was covered with sand to a depth of 5 cm. The temperature near the ground was constantly 30·5–31° C., and reached 37–38° C. under the ceiling.

Stridulation noises were recorded through an electrostatic, directive microphone (Melodium type 515 C, with a linear sensibility curve of 40–15,000 c/s $\pm$ 1 dB) on a tape recorder (Tolana, with a frequency range up to 40,000 c/s). The oscillographic analysis was carried out with a " Cossor " cathode-ray oscillograph and frequency determination was done with a " CNET " analyser (System Pimonov). The sound intensity was measured with a " LEA " dB-meter. For other purposes the following microphones were used : an electrodynamic, non-directive microphone (Melodium, type 55A) with a

frequency range of 50–15,000 c/s and a quartz crystal-microphone connected with a pre-amplifier and with a range of 15,000–100,000 c/s.

III. Observations and Experimental Results

(1) *Mandibular Noises*

The Desert Locust produces noises by rubbing the two mandibles against each other. It is, however, still uncertain whether this kind of stridulation has a sexual significance. It can be observed in both sexes, occurs relatively infrequently and is heard when an insect is alone rather than in company of an individual of the opposite sex.

(2) *Wing Stridulation*

All the Catantopinae so far investigated have in common a sudden copulation attack, where the male tries to get upon the back of the female. With the exception of *Calliptamus italicus*, which makes mandibular noises, assaults are made without stridulatory sounds. The female usually reacts with defensive movements of the hind femora and tibiae. However, in *Schistocerca* a male is sometimes observed to take a position very near to the female, either posteriorly, anteriorly or anterolaterally. Shortly before jumping upon her, he produces short, sharp sounds, which increase in number during the attack. These can also be heard when the male merely sits on the female's back in a sort of pre-copula or tries to copulate.

More frequent is another kind of stridulatory sound which appears either in combination with the " short sounds " just mentioned, or alone : these are long sequences of whizzing noises, following each other after long irregular intervals. Plate I, figures 1–4 show the audiospectrograms and oscillograms of both kinds of sounds.

The " short sounds " last 0·1–0·2 sec. and the " long sounds " 1–6·0 sec. (30 measurements), their intensity being 40–45 dB when the singing insect is 10 cm. away from the microphone. The frequency distribution ranges in both cases from 0–23 kc/s and may possibly be wider. As far as can be seen from the audiospectrograms, the ultrasonic part is relatively weak compared with the audible range.

The stridulation sounds are produced exclusively by means of the fore and hind wings and not by the hind femora and elytra. In the resting position the left elytron overlaps the right one in the anal area to form a roof-like covering with steeply sloping sides, completely enclosing the more delicate hind wings. The " short sound " is made by slightly raising both pairs of wings, which beat a few times against each other and are then brought back into their original position. According to the oscillogram, their movements have a frequency of 1/50–1/100 sec., that is, they cannot be followed with the naked eye. For closer investigation cinematographic records are therefore essential.

The movements concerned in the production of the " long sound " are more difficult to observe : both the wing-pairs remain in the resting position and vibrate with an amplitude of 1–2 mm. in a horizontal direction. When observed from above, the tegmina appear blurred during stridulation. Sometimes the " long sound " is accompanied by a rapid vibrating of the hind femora

with a very small amplitude in the lateral direction. These movements are only performed when the hind tarsi do not touch the ground, otherwise they are suppressed.

(3) *Stridulatory Mechanisms*

Some simple operations (on about 25 males) gave further evidence about the nature of these stridulatory mechanisms.

It was found that amputation of both the hind wings had almost no detrimental effect on sound-intensity and quality. If, however, the narrow anal areas of the elytra which rub against each other were cut off, intensity dropped markedly. As a further step one whole elytron was removed. Although the sound intensity then became very weak, a noise was still audible, caused by the vibration of the rigid elytron itself.

The beginning of the " long sound " is remarkable in that it starts suddenly, the fore wings being rapidly lifted slightly and brought outwards a few degrees in one movement, thus providing enough space in which to oscillate. If an insect stridulates with the hind wings only remaining, the intensity is very appreciably less and a soft noise is heard ; the wings also vibrate horizontally in their longitudinal axis, their ends beating against each other. Sometimes under these conditions the hind wings unfold and make flying movements ; more frequently, however, they are only half unfolded when stridulation starts and are brought back during the process into their original position. Therefore, in a normal insect the tegmina hold the hind wings together and prevent them from opening during stridulation. This means that the two pairs of wings touch not only when motionless, but also very intensively during stridulation. Whether or not the elytra and hind wings vibrate synchronously can only be determined by making film records, but amputation of an elytron and a hind wing, one from either side, shows that the remaining parts begin and end the oscillation together. The hard structure of the elytra and the marked diminution of the sound-intensity after their amputation suggest that they function as a resonance-body. The same is true for the tegmina of some Truxalinae (Loher, 1957).

For the " short sound " the two pairs of wings also collaborate, but the sound is also produced when one pair is lacking. The " long sound " is always accompanied by a lively beating of the antennae and the two pairs of palpi, whereas " short sounds " usually occur without such movements.

So far as present knowledge extends, the occurrence of these two forms of stridulation in the sexual behaviour of *Schistocerca gregaria* is unique, which gives them a certain significance. The presence of the " short sounds " before and during copulation attack suggests that they are so-called assault-sounds (*Anspringslaute* (Jacobs, 1953)). In the Catantopinae, only *Calliptamus italicus* has been reported to stridulate on such occasions (Faber, 1949), the sound being produced by means of the mandibles.

The " short sounds " are also involved in the expression of another form of behaviour more often represented by " long sounds ". Both forms of stridulation can then occur either together (Pl. I, fig. 5) or alone (Pl. I, figs. 3, 4) and are observed in a male on the back of a female ; the sounds are only very occasionally emitted by single males which have been repulsed when they tried to copulate.

The female attacked makes either defensive movements or a series of sudden abrupt movements, which consist of running around and stopping suddenly, shaking the male and causing it to stridulate with long or short sounds. The male very often emits long sounds when it tries to copulate and rubs its abdomen along the side of the female in order to reach the genital opening.

Less frequently stridulation is released in a copulating male by the mere appearance of a second male, but " long sounds " are often emitted when it is actually attacked by the second male. After a successful defence, the copulating male again produces the " long sound ".

The two acoustical reactions just described should very probably be classed as disturbance noises (*Störungslaute* (Jacobs, 1953)).

(4) *The Defensive Reaction*

So far we have seen that disturbance noises have been connected with sexual behaviour, but more often than not reactions to disturbance are soundless and not limited to sexual behaviour.

A defensive reaction in both the male and female is released mainly by tactile stimuli and consists of kicking movements of the hind tibiae. If the insect is touched at the proximal ends of the elytra, the tibiae are flung backwards, but when stimulated at the head the hind femora are brought into a vertical position and even obliquely forwards, so that the kick of the tibiae is directed towards the source of the disturbance. Occasionally under these circumstances the aggressor is bitten with the mandibles.

(5) *The Femoral Vibration Movements*

The mechanism of defence described above is regularly followed by the so-called " vibration " movements, which in this insect are one of the most important manifestations of behaviour and can be observed particularly often in the relations between male and female, although, as will be seen later, the vibration reaction is not always connected with defensive movements.

The vibration reaction is executed by the two femora, posed at a slight angle from the body. In this position they make rapid vibratory movements which consist of two components, namely a lateral and a relatively smaller antero-posterior movement. The tibiae are held away from the femora, sometimes even at right angles. The tarsi rarely touch the ground, though this may happen occasionally. The amplitude of the vibration and its duration seem to vary with the state of excitement of the insect, which is possibly dependent on the quality and quantity of the releasing stimulus.

In action the hind femora never touch the elytra. In ten males and females studied it was shown that during the leg vibration no sound was produced. Two microphones with a frequency sensibility range of 50–15,000 and 15,000–100,000 c/s were held 2 cm. from the vibrating insect and connected by an amplifier to a cathode-ray oscillograph in order to record visually the sounds produced. All experiments were entirely negative. The vibration reaction is accompanied, like a " long sound ", by lively movements of the antennae and the two pairs of palpae. It occurs in both sexes, although more often in the females. The main releasers are tactile stimuli. Whenever a mature male

and female touch each other during an attack, while in pre-copula, or during a copulation attempt, the contact provokes vibration reaction in both parties.

In order to demonstrate how often the random movements of the female in copulation are the cause of the vibration reaction of the male, the female was replaced by my finger, which was readily accepted because the male at once started copulatory movements. Only slight motions of the finger caused the vibration reaction in a quietly sitting male.

The male and female reach the climax of excitement under different conditions. The male sitting on the female's back is seen to vibrate with the greatest amplitude when attacked by another male. Defensive and vibration movements follow each other continuously and cease only after a variable time, when the aggressor has been repulsed. The female shows the strongest agitation after it has successfully pushed the male off its back, which happens only after a tough fight. The vibration is then performed with a vehemence not observed on other occasions and may continue for 2–3 minutes, whereas normally it does not last longer than 30 seconds.

The tactile stimuli need not necessarily come from the opposite sex because vibrations among groups which consist only of males or females have been observed. They can even be provoked by touching the insects lightly with a fine brush on the head, prothorax, elytra or abdomen.

Visual stimuli are the second category of releasers of this reaction. When a female meets a mature male it stops, vibrates the femora, with the antennae and palpi moving fast, and runs away. In the case of two slowly approaching males usually nothing happens, but this more or less indifferent behaviour changes immediately if one of them is on the back of a female, either in copulation, or only sitting there. Each approaching male is regarded as a disturber and at a distance of 10 cm. the vibration movements start, increasing in intensity as the intruding male comes nearer. The female sometimes joins the copulating male in the vibration. It will soon cease, however, if the approaching male stops and remains motionless. Even with the intruding male sitting 1 cm. in front of the couple, the copulating male will soon calm itself and cease to be interested, but slight movements of the single male again release the vibratory reaction.

Mature males isolated for more than eight days and then placed with females will jump upon everything which moves quickly. Fast moving males are then frequently attacked as well. The aggressor does not realise its error for a long time, because the attacked male behaves as would a female, performs defensive and vibratory movements and after repulsion vibrates again for a while. Wooden dummies, which very roughly imitate the shape of a locust, never fail to release a vibration reaction in a copulating male when they are merely swung in front of the couple. Motionless dummies, however, are ineffective. The same stimuli, moved before the male when alone, provoked assaults.

These examples make it quite clear that " motion " is an essential factor in the visual releasing mechanism. In this connection it is interesting to note that yellow colouring, which is that of the mature males, seems to improve the quality of the dummies. If the compound eyes and ocelli of individuals are covered with black lacquer there are no vibration movements in response to the visual stimuli described above.

Acoustical stimuli, such as the assault sounds before copulation attack, have also a releaser effect, but they are certainly less important than visual factors.

Other results, (Loher, 1958), strongly suggest that certain olfactory stimuli are also able to provoke vibration movements in the male and in the female.

The reactions described above are probably primarily expressions of disturbance. The vibration reaction serves as a defensive movement, although less than the active defence reaction with its directive effect. It may help to make the copulation attack more difficult, *e.g.* when the male assaults from the side it hardly ever succeeds in getting upon the back of the female. In addition, the vibration reaction is likely to serve as a visual warning against aggressors. Females which have successfully repulsed a male and vibrate afterwards for an exceptionally long time are very rarely attacked during this period or immediately afterwards.

IV. Discussion

An account has been given of stridulatory mechanism of a kind previously unknown in Acridoidea. Norris (1954) briefly mentioned wing stridulation in *Schistocerca*, but did not investigate it. It is suggested that this method of sound production is primitive and confirms once again that a new function does not necessarily need a new organ if one is already present (Zeuner, 1934)—in this case the wings—which can perform it. Very probably wing stridulation has developed from wing beating, as is suggested by some of the experiments described above.

So far as is known, wing stridulation can be found only in *Schistocerca* amongst the Acrididae but it is the principal method of sound production in Tettigoniidae, where a row of teeth on a tegminal vein is scraped by a sclerotised part of the opposite tegmen. There is, however, a significant difference between the stridulatory mechanism of the Tettigoniids and *Schistocerca*. The Tettigoniids use only the elytra, which bear the stridulatory organ, for stridulation, whereas in *Schistocerca* both pairs of wings are active and the fore wings show neither a strong development of the veins nor any other form of specialisation which would suggest a sound producing organ.

It is perhaps noteworthy that examination of fossils of Tettigoniids in the upper Palaeozoic did not reveal any sound producing organs (Zeuner, 1934). Whether they stridulated in the same manner as *Schistocerca*, if at all, is impossible to determine, and whether the methods of sound production in recent Tettigoniids and *Schistocerca* were of the same evolutionary origin is beyond the scope of the present work.

Assault-sounds, disturbance noises and defensive reactions, which are found so frequently in *Schistocerca*, have been reported from a great number of shorthorn grasshoppers (Faber, 1949, 1953; Jacobs, 1953). The acoustical reactions never have a complicated structure, unlike the highly differentiated songs of, for instance, the courtship behaviour of Acridinae. Because of their wide distribution they are regarded as phylogenetically very old forms of behaviour (Jacobs, 1953). The same applies to the vibration movements, with their significance in the range of disturbance, defence and warning, which are found with similar features in some Acridinae and regularly in Oedipodinae

and Catantopinae (Faber, Jacobs). Nevertheless several differences become apparent when they are compared with each other ; *Schistocerca* never vibrates for less than 2·5 seconds, usually 20–30, and sometimes as long as 2 minutes, whereas similar movements in other Acrididae (*stummes Schenkelschütteln*, soundless shaking of the femora, (Jacobs, 1953)) do not exceed 1 second.

We have, therefore, in the vibration reaction a form of behaviour which is not stereotyped but extremely variable in its duration. It is not limited to sexual behaviour as are the similar movements in Acridinae, and seems to occupy a more important place in the life of *Schistocerca* than in any other species so far studied. A further indication of its primitiveness may be the non-specificity of its releasers, which can be tactile, visual, acoustical or olfactory.

Primitive mechanisms of behaviour are not only interesting in themselves, but may also help in understanding the origin and evolution of the complex behaviour patterns of the higher Acridoidea. Further studies of the behaviour of Catantopinae may therefore be of particular value.

Acknowledgments

I would like to record my sincere thanks to Dr. C. T. Lewis, Dr. B. P. Uvarov and Professor Dr. W. Jacobs for helpful criticism of this paper. I am also indebted to Dr. R. G. Busnel for hospitality in his Laboratoire de Physiologie Acoustique in Jouy-en-Josas (France) for a period of one month. Finally I wish to thank Professor O. W. Richards for facilities provided at the Imperial College Field Station during the tenure of a Senior Research Award granted by the Anti-Locust Research Centre.

Author's note :

After the termination of these investigations I have learnt that during 1953–57 Miss I. Drost, a student of Prof. Dr. Faber, Tübingen, has analysed the sexual behaviour of *Schistocerca gregaria* Forsk., but has not yet published the results. I am informed that part of her work coincides with part of mine and that our observations are similar.

Summary

1. Males and females of the Desert Locust *Schistocerca gregaria* (Forsk.) produce noises by rubbing the mandibles against each other, but the sounds appear to have no significance in sexual behaviour.

2. Two other types of noise, consisting of " short " and " long " bursts of sound respectively, are produced by stridulation of both pairs of wings in the male.

3. The mechanisms of sound-production have been investigated and physical analyses of the sounds have been made.

4. Behaviour observations suggest the " short sounds " to be assault-sounds, but they are also, like the " long sounds ", an expression of disturbance. Both sounds are associated with sexual behaviour.

5. Individuals of both sexes are provoked to make a defensive reaction when touched by other locusts. This reaction consists of directed kicking movements of the hind tibia. Biting occasionally occurs.

6. An entirely different response, which may be released by tactile, visual,

acoustical or olfactory stimuli, consists of a vibration movement by the hind femora. This vibration reaction is one of the more important and frequent manifestations in the life of *Schistocerca*. The movement has a large lateral and a smaller antero-posterior component. It is proved experimentally that neither audible nor ultrasonic sounds are made during this reaction, which is an expression of disturbance and may also serve as a defensive or warning reaction.

7. Wing stridulation is compared with the stridulatory mechanism of Tettigoniidae and the vibratory reaction with similar movements in other Acrididae.

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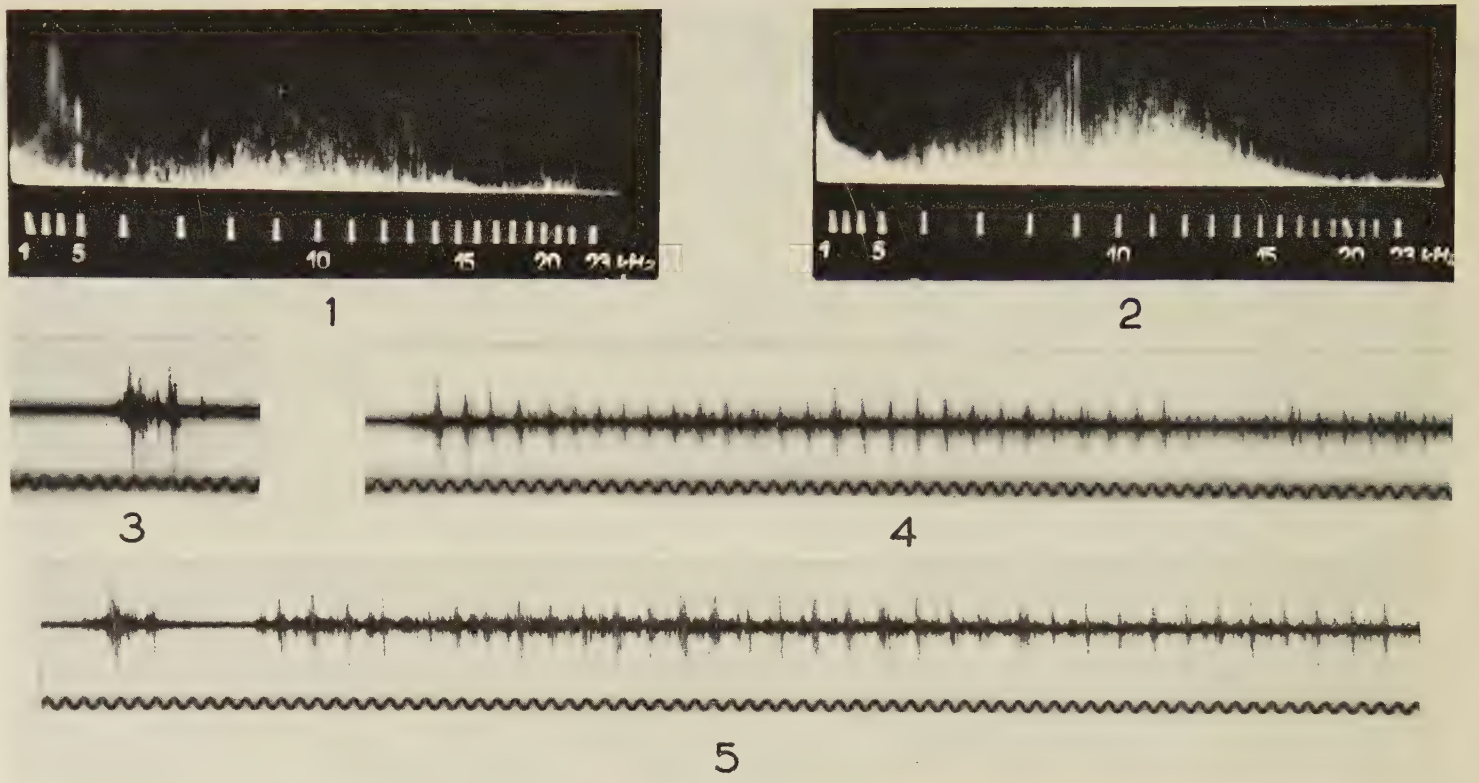

Schistocerca gregaria Forskål : Records of stridulation noises.

Figs. 1, 3.—Audiospectrogram and oscillogram of a " short sound ".
Figs. 2, 4.—The same of a " long sound ".
Fig. 5.—Oscillogram of a combination of both types of sounds.
Timing wave in all cases 50 c/s.

THE MAXILLARY GLANDS OF SOME COLEOPTERA

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Introduction

Our knowledge of the gnathal glands of the Coleoptera is fragmentary and the morphological nature of the glands which have been described is not properly understood in all cases. Berlese (1909) referred to the presence of "paired labial glands" in the adults of Chrysomelidae and *Blaps* and in larvae of *Coccinella septempunctata* L., with separate lateral openings for each gland in the latter; and, long before, Dufour (1840) had described a pair of tubular glands with a common opening in *Pyrochroa*. Murray and Teigs (1935) mentioned a pair of tubular glands, each with a separate opening, in *Calandra oryzae* L., and Pradhan (1936) gave an account of similar glands in *Epilachna indica* L. Again, Gupta (1937) described in detail paired "salivary glands" in 16 species of Tenebrionidae. He found each gland opening separately in the preoral cavity between the hypopharynx and the maxilla of its side and demonstrated the presence of mucin in them by the mucin-haematin test. He concluded that such glands are usually present in the Tenebrionidae and attributed a salivary function to them. Soon after, Pradhan (1939) showed the presence of several kinds of head glands in the Coccinellidae and, according to the position of their openings, he referred to them as mandibular, maxillary, labial and labral. The present observations were made with the object of extending the available information and ascertaining the function and morphological status of glands of this kind.

Material and Technique

Gnathal glands of the following beetles are described:

Tenebrio molitor L. (Tenebrionidae): larva and adult.
Tribolium confusum Duval (Tenebrionidae): larva and adult.
Phaedon cochleariae Fab. (Chrysomelidae): larva and adult.
Galeruca tanaceti L. (Chrysomelidae): larva.
Rhagium bifasciatum Fab. (Cerambycidae): larva.

The study has been based mainly on dissections under a high power binocular microscope after staining vitally with methylene blue, and on microscopic preparations of whole glands after fixation and staining with borax carmine and Delafield's haematoxylin. For the detection of amylase in the salivary glands, glands of a large number of adults or larvae of *T. molitor* were removed quickly and ground in a few drops of toluene; the extract thus prepared was incubated with two or three drops of 0·5 per cent. starch solution in a microtube at 20° C. for 24 hours and then subjected to the iodine test. A control was treated similarly and all tests were repeated to confirm the results.

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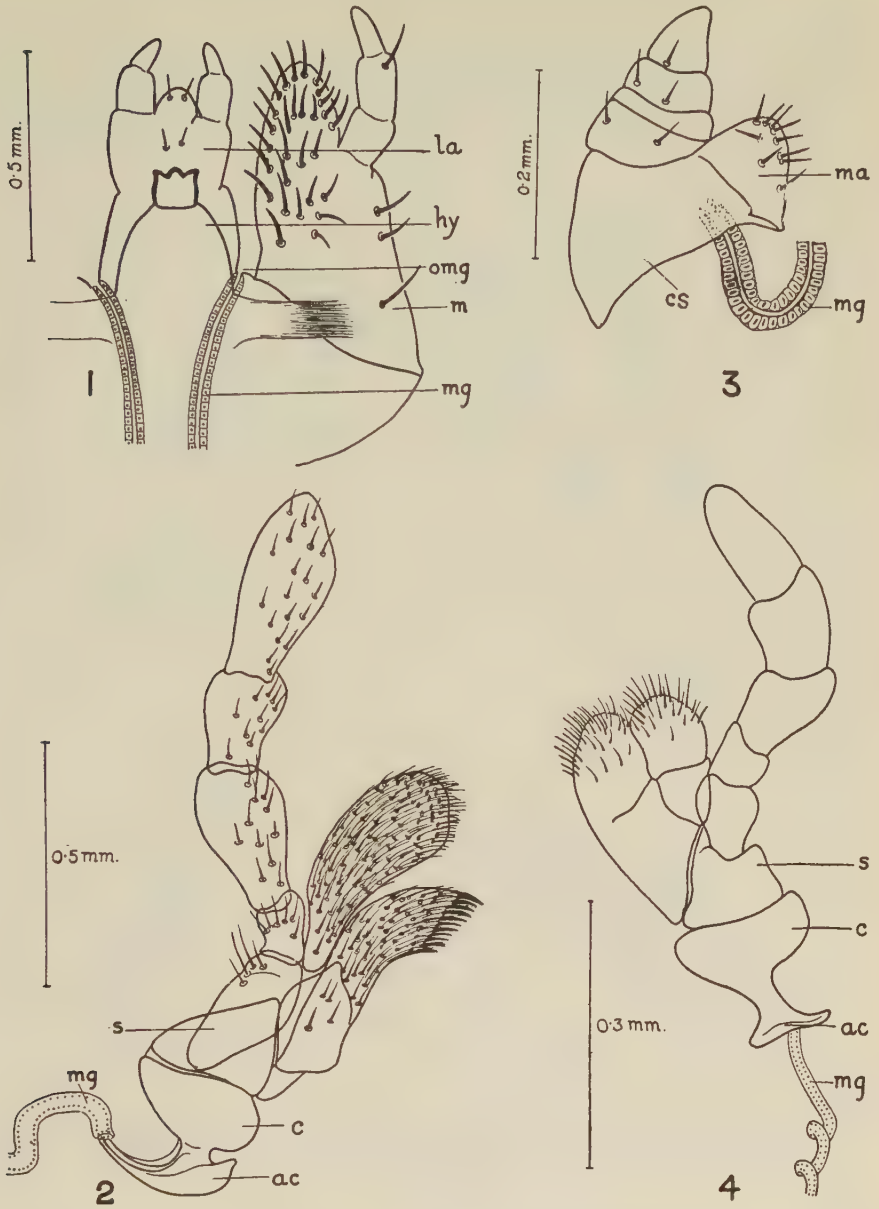
Observations

A pair of long, slender, tubular, unbranched, almost transparent glands were noted in all the larvae and adults mentioned above. In the two Tenebrionids, the condition of the gland differs slightly but significantly in the larvae and adults. In the larvae of both species, the glands run along a more or less straight course. Starting from the region of the prothoracic spiracles, each proceeds anteriorly along the ventral tracheal trunk which supplies the head. As the two glands approach the ventral nerve cord they pass between the paired longitudinal connectives and run forward close to each other beneath the suboesophageal ganglion. In the head, they run ventral to the foregut and finally diverge laterally again when each opens separately on the membrane in the angle between the labium and the maxilla of its side (fig. 1). In the adults, the glands are more slender and much longer, but at the same time they are withdrawn completely into the head, in which they remain convoluted. They are, therefore, not seen in the prothorax and for this reason they are frequently overlooked. The most important feature of the adult gland is its direct association with the maxilla. In *Tenebrio*, where the structures can be more accurately determined on account of their large size, the cardo is wedge-shaped and produced posteriorly into a thin, pointed, grooved apodeme which is directed laterally into the cranial cavity (fig. 2). The duct of the gland is clearly seen terminating at the apex of the apodeme and the cavity of the duct is apparently continuous with the groove of the apodeme.

In *Phaedon cochleariae* the larva possesses a similar pair of glands which are again situated in the prothorax and run along the ventral tracheal trunk supplying the head. But they do not pass beneath the nerve cord and run ventrally to the oesophagus in the anterior part. On reaching the head, each turns laterally and enters the maxilla of its side (fig. 3). In this insect, the cardo and stipes are not differentiated from each other, and the duct of the gland, entering the large ring-like cardo-stipital sclerite from behind, opens on the epidermis within it. On tearing the sclerite open and separating the epidermis from it, the opening of the duct on the latter can be confirmed, but owing to the heavy pigmentation of the sclerite the external opening could not be seen. In the adult *Phaedon* (fig. 4), the condition closely resembles that of the adult *Tenebrio*. In this case, the cardo is produced into a hammer-shaped, posteriorly directed apodeme, and again, as in *Tenebrio*, the duct terminates at the posterior margin of this apodeme. On account of the heavy sclerotisation and dark colour of the apodeme, the presence of a groove in it could not be confirmed.

In the larva of *Galeruca tanaceti* the glands are relatively much longer. Their distal ends lie anteriorly in the prothorax, from which each runs posteriorly in the lateral part of the prothoracic cavity. On reaching the posterior region of the prothorax, it again turns forward and then pursues nearly the same course as the gland of *Phaedon*. The opening of the gland is also similar, being situated on the epidermis lining the cardo-stipital sclerite of the maxilla.

In the larva of *Rhagium bifasciatum*, the glands again start from the postero-lateral part of the prothoracic cavity, near the prothoracic spiracle and run along the ventral tracheal trunk to the head, as in *Tenebrio*, but they do not run beneath the nerve cord. Their openings also, as in *Tenebrio*, are



FIGS. 1–4.—(1–2) *Tenebrio molitor :* (1) labium, hypopharynx and right maxilla of larva, with part of the maxillary gland, showing the openings of the latter ; (2) maxilla of adult, with part of the maxillary gland. (3–4) *Phaedon cochleariae :* (3) maxilla of larva, with part of the maxillary gland ; (4) maxilla of adult, with part of the maxillary gland.

ac, apodeme of the cardo ; *c*, cardo ; *cs*, cardo-stipital sclerite ; *hy*, hypopharynx ; *la*, labium ; *m*, maxilla ; *ma*, mala ; *mg*, maxillary gland ; *omg*, opening of the maxillary gland ; *s*, stipes.

situated on the membrane in the angle between the maxilla and labium on each side.

The histology of the glands (fig. 5) is very simple in all these cases. Each consists of a layer of secretory cells arranged on a basement membrane and invested on the inner surface with a thin and uniform layer of cuticle. The nuclei are strongly basophil and compact, being full of chromatin granules.

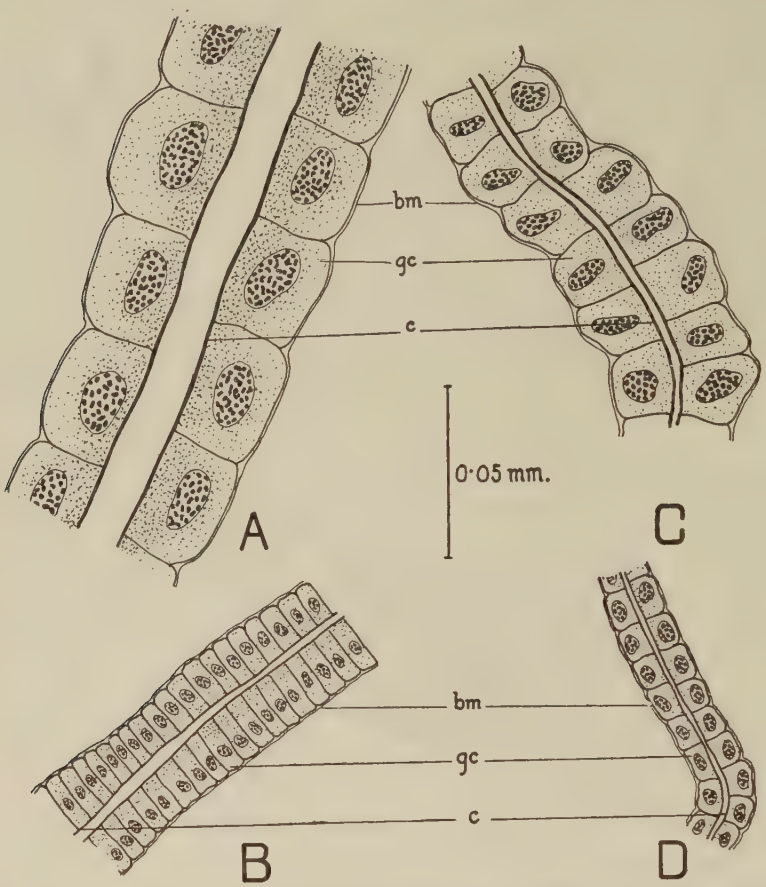


Fig. 5.—Parts of the maxillary glands to show their histological structures : (A) *T. molitor* larva ; (B) *T. molitor* adult ; (C) *P. cochleariae* larva ; (D) *P. cochleariae* adult. *bm*, basement membrane ; *c*, cuticle ; *gc*, secretory cells.

They are oval, rounded or disc-shaped and do not show lobulations. The cytoplasm is uniform and without vacuoles. An interesting feature of the histology of these glands is the fact that the cells of the adult gland are very much smaller than those of the larval gland, so that the diameter of the latter is about twice that of the adult.

To check the possible salivary function of the glands, the iodine test for the detection of amylase was performed with the gland extracts of adults and larvae

of *Tenebrio* separately. After incubating the starch substrate with the gland extract for 24 hours at 20° C., the presence of the starch was again demonstrated by the iodine test, showing that amylase, which hydrolyses starch, is absent from the glands.

Discussion

It can be seen, therefore, that the gnathal glands are fundamentally similar in the larvae and adults studied. In all cases, they are slender, tubular, made of a single layer of cells and lined internally by cuticle ; in all they are limited to the prothorax or head and do not extend into the metathorax ; furthermore, they always have separate openings and do not unite to form a common duct or open by a common aperture. It may be mentioned that in other orders of insects, the " salivary " glands generally consist of the labial glands, which usually unite to form a common duct opening on the labium beneath the hypopharynx, whereas the maxillary glands are directly associated with the maxilla. Gupta (1937), who described similar paired tubular glands in 16 Tenebrionids, stated that they open in the extra-oral cavity separately on the two sides, and because he noted mucin in them he called them " salivary glands " and compared them with the glands which Dufour (1840) had described in *Pyrochroa* as possessing a common duct similar to the salivary glands of other orders. Pradhan (1936) found similar glands in *Epilachna*, the openings of which are situated separately between the maxilla and labium beneath the sides of the hypopharynx. He subsequently (1937, 1939) confirmed these as maxillary glands, having found separate glands which opened on the labium and which he, therefore, regarded as labial glands. The openings of the glands in the larvae of the Tenebrionids and *Rhagium* lie between the hypopharynx and maxillae but any doubt regarding the morphological nature of the glands arising from the position of the openings is removed when account is taken of their position in the adults of the two Tenebrionids and the adults and larvae of the Chrysomelids, in all of which the openings are situated in the maxillae. Murray and Teigs (1935) also stated that the paired glands of the larvae and adults of *Calandra oryzae* open on the maxillae. While the possibility of true labial glands having separate openings cannot be ruled out, one can hardly fail to note that the only instance where such a condition of the labial glands has been reported in the Coleoptera is in the Coccinellids (Pradhan, 1939), and in these the glands have an " elaborate system of ducts and ductules " and open " separately at the level of the proximal margin of the prelabium, between it and the hypopharynx ". This structure and the situation of the openings is very different from that of the tubular glands described above although Pradhan designates such glands as the maxillary glands. It can, therefore, be stated that the simple tubular paired glands of the Tenebrionidae and certain Curculionidae, Coccinellidae, Chrysomelidae and Cerambycidae are maxillary glands which should not be confused morphologically with glands having a common opening, as in *Pyrochroa coccinea* L., or those with paired openings on the labium such as accompany the labial glands in Coccinellids. These latter may be true labial glands and are apparently very rare in the Coleoptera, while the maxillary glands appear to be much more widely distributed than was hitherto believed. The fact that the tubular glands are devoid of an amylase further proves that these are not salivary in nature and helps

to distinguish them from labial glands in general. It may perhaps be added that the maxillary glands of *Tenebrio* larvae were wrongly described by Stellwaag-Kittler (1954) as prothoracic endocrine glands (*see* Srivastava, 1959).

Acknowledgments

I am very grateful to Professor O. W. Richards for providing me with laboratory facilities and to him and Mr. R. G. Davies for their valuable suggestions and for going through the manuscript.

Summary

Paired tubular glands opening separately in the angle between the labium and the maxilla have been noted in the larvae of *Tenebrio molitor* L., *Tribolium confusum* Duval and *Rhagium bifasciatum* Fab. and similar glands opening on the maxillae have been recorded in the larvae of *Phaedon cochleariae* Fab. and *Galeruca tanaceti* L. and in the adults of *T. molitor*, *T. confusum* and *P. cochleariae*. The glands in the adults and larvae of *T. molitor* do not produce amylase. On account of their separate openings, association with the maxillae and lack of amylase, they are regarded as maxillary glands which do not secrete saliva.

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A BIOLOGICAL VARIANT OF *ORNITHODOROS MOUBATA* MURRAY (IXODOIDEA : ARGASIDAE) FROM SOUTH AFRICA

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Contents

1. Introduction

In 1955 a collection of *Ornithodoros moubata* Murray, obtained from native huts at Groot Marico in the Western Transvaal, was received from Dr. Botha de Meillon of the Institute for Medical Research, Johannesburg, and subjected to routine examination for biological characters with a series of East African strains (Walton, 1957, 1958*a* and *b*).

These South African *O. moubata* were not quite so robustly built as the East African strains. Their legs appeared to be more slender and of a paler yellowish tint and, particularly when engorged, the body was dove grey rather than the browner or dark grey shade of the East African strains. The exuviae were also paler and more delicate. These appearances were maintained in numerous generations up to 1957, when further cultures were received from Dr. F. Zumpt of the South African Institute for Medical Research, who was engaged in a study of the ticks of the Bechuanaland Protectorate (Zumpt, 1958). In personal communications Dr. Zumpt states that of 20 widely scattered collections of domestic *O. moubata* obtained in Bechuanaland and South West Africa, only one was infected with *Spirochaeta duttoni*. The collections he sent from Lehututu, Ramaquabane, Kokojane and Jackales in Bechuanaland and Windhoek and Runta in South West Africa are very widely dispersed representative collections of this rarely infected strain of *O. moubata*.

Early in 1958 an additional collection of *O. moubata* from native huts in Nova Lisboa in Angola was received from Dr. V. A. S. Dias, Director of Angolan Veterinary Services.

Observations on certain biological characters of these eight cultures were made at the Institute for Medical Research, Mwanza, Tanganyika, and have led us to the conclusion that these cultures of *O. moubata* all belong to a

distinct biological variant. In addition, it should be mentioned here that the distribution of this tick in native huts in the central and western areas of South Africa (Zumpt, 1958) is far more continuous than previously suspected (Leeson, 1952), despite the general aridity of the area and the existence there of extensive deserts (Walton, 1957).

The situation of the localities where the *O. moubata* used in these studies were obtained is shown in figure 1.

Fig. 1.—Sketch map of South Africa showing the places mentioned in the text. The October 70° F. isotherm, and the 20 inch and 40 inch isohet are shown (after Kendrew, 1953). Kokojane is situated in the Kalahari Desert between Groot Marico and Lehututu and approximately on the 20 inch isohet. Jackales is situated north of Ramaquabane near the Southern Rhodesian border. (*See* Walton, 1957 : 690 ; and Leeson, 1952 : 408.)

2. Frequency of Feeding and Number of Nymph Stages

In 1956 it was discovered that an unusually high proportion of the males of the Groot Marico, Transvaal, culture required only three feeds, and a corresponding number of nymph stages, to reach maturity (Walton, 1958*b*) and, as further information became available, it was discovered that no females of the East African strains had ever matured after less than four feeds, whereas one-fifth of the Groot Marico females required only three feeds. Moreover, while it was rare for a Groot Marico female to require five feeds, anything from 30–65

per cent. of the East African strains required five feeds, some required six and a small proportion required seven and, while a proportion of the males of all East African strains required five feeds to reach maturity, this number was not required by the males of the Groot Marico strain.

The number of nymph stages required by some strains of *O. moubata* was given in Walton (1958*b*), and the original data derived from the Groot Marico strain are repeated below in Table I.

TABLE I.—*The number and percentage of feeds and nymph stages required to reach maturity by both sexes of the parent generation of the domestic strain of* O. moubata *from Groot Marico, Transvaal*

		Number					%				
No. of feeds		3	4	5	6	7	3	4	5	6	7
Groot Marico, Transvaal	♂	220	62	0	0	0	78	22	0	0	0
	♀	55	245	1	0	0	18	81	0·3	0	0
	Total	275	307	1	0	0	47·2	52·6	0·2	0	0

These observations have now been made on a total of some 10,000 individual *O. moubata*, including 2306 individuals of the South African strains, and 7685 of the East African strains. The original observations made on the Groot Marico strain hold true, as will be seen in Table II.

TABLE II.—*The number and percentage of feeds and nymph stages required to reach maturity by all strains of the South African domestic* O. moubata *and all strains of both wild and domestic* O. moubata *from East Africa*

		Number					%				
No. of feeds		3	4	5	6	7	3	4	5	6	7
All South African strains	♂	988	157	0	0	0	86·3	13·7	0	0	0
	♀	125	1027	9	0	0	10·7	88·5	0·8	0	0
	Total	1113	1184	9	0	0	48·3	51·3	0·4	0	0
All East African strains	♂	58	2611	939	122	4	1·5	70·0	25·2	3·3	0·1
	♀	0	1608	1921	418	8	0	40·6	48·6	10·6	0·2
	Total	58	4219	2860	540	12	0·7	54·8	37·2	7·0	0·2

This characteristic behaviour of the South African strains was shown to be hereditary in a random sample of nymphs derived from five males and five females (themselves taken as a random sample) of the generation of the Groot Marico strain whose moulting data are given in Table I. The result of rearing these nymphs is given in Table III.

TABLE III.—*The number and percentage of feeds and nymph stages required by a first filial generation of the Groot Marico strain of* O. moubata *to reach maturity. Compare with Tables I and II*

		Number					%				
No. of feeds		3	4	5	6	7	3	4	5	6	7
Groot Marico	♂	158	28	0	0	0	85	15	0	0	0
	♀	11	159	4	0	0	6	92	2	0	0
1st filial generation	Total	169	187	4	0	0	47	52	1	0	0

Details of the number and percentage of feeds and nymph stages required by the Lehututu, Ramaquabane, Kokojane, Jackales, Runta and Windhoek strains are given together in the Appendix. Time did not allow similar data for the Nova Lisboa strain from Angola to be obtained.

3. Mode of Feeding and Secretion of Coxal Fluid

Details concerning the appearance during feeding, the duration of feeding, and the mode of secreting coxal fluid in the East African variants of *O. moubata* are given in Walton (1958*b*). Only two females of the Groot Marico strain were tested in the original observations made in 1957, and these gave somewhat different results from the East African strains. These females attached readily and assumed a shape somewhat reminiscent of the " warthog-burrow " wild East African strains (*see* fig. 2 and also fig. 4 in Walton, 1958*b*). The anterior pair of legs were extended well forward and strongly recurved. The venter was convex and contacted the skin of the rabbit's ear used in the test. Coxal fluid was delayed in appearance for 13 minutes following attachment in one female and appeared within 5 minutes of attachment in the other. At maximum engorgement, when the skin was fully distended, the posterior height was greatest and the posterior width less than the anterior width. Viewed laterally they differed from the " warthog-burrow " strains of *O. moubata* in being flatter in the anterior dorsal aspect, and when viewed vertically their shape was more oblong-oval than broad-oval. Frontal contractions were extremely feeble and frequently unilateral and a dimple appeared half-way along the dorsal inner sublateral depressions. Coxal fluid was secreted up to the moment of detachment, which was sudden, as in the " warthog-burrow " strains. After detachment the dove-grey tint of the body was most obvious. Total feeding time in one female was 28 minutes, but was 59 minutes in the other.

In 1958 ten more unfed and unmated females of the Groot Marico strain were " test fed ". The general appearance was as described above. Coxal fluid was first noted at from 6 to 13 minutes after attachment and total feeding time varied from 28 minutes to 70. The mean feeding time was 39 minutes and coxal fluid was excreted during 75 per cent. of that time. A distinct transverse dorsal hump, seen in the early stages of engorgement (fig. 2 (*a*)), and again towards the end of the feed when the tick is deflating before detachment, was first noticed during this test. Unilateral secretion of coxal fluid was noted in several females as well as transient anterior unilateral contractions. The day after the feed the females were elliptical in lateral view, ventrally slightly concave and slightly thicker anteriorly in contrast to the anteriorly humped appearance of the " warthog-burrow " strains and the pear shape of the East African domestic strains (fig. 2 (*e*)). At no time was coxal fluid seen to wet the integument of the tick.

Ten unmated and unfed males and females of the Lehututu strain were " test fed ". This test was carried out rather too soon after the final moult and the larger females derived from the fourth stage nymphs were not sufficiently hungry to give a clear-cut result. The smaller females derived from the third stage nymphs behaved very similarly to the Groot Marico strain, but only one of the larger females assumed the typical elongated oblong-oval shape at

maximum distention. The mean feeding time of the females was 43 minutes; coxal fluid was excreted for 63 per cent. of that time and there was no cessation of flow up to the time of detachment. The ten males fed for a mean time of 36 minutes and secreted coxal fluid for 61 per cent. of that time.

Six females of the Ramaquabane strain were exactly similar in appearance to the Groot Marico strain when tested. Mean feeding time was 30 minutes and coxal fluid was excreted for 62 per cent. of that time, its appearance being delayed on the average for 12·5 minutes. Three females of the Runta strain also closely resembled the Groot Marico strain. Mean feeding time was 40 minutes. Coxal fluid was secreted for 60 per cent. of that time but its appearance was delayed for a mean of 15 minutes. Ten females of the Nova Lisboa, Angola, strain also gave very similar results, except that frontal contractions were slightly more obvious than in the preceding strains. Mean feeding time was 28 minutes, and coxal fluid was excreted for 61 per cent. of that time. Two females from the Windhoek strain gave somewhat aberrant results (if the results obtained from the Groot Marico strain are regarded as typical), since the appearance of coxal fluid was markedly delayed in both specimens for 26 and 30 minutes out of feeding times of 60 and 43 minutes respectively.

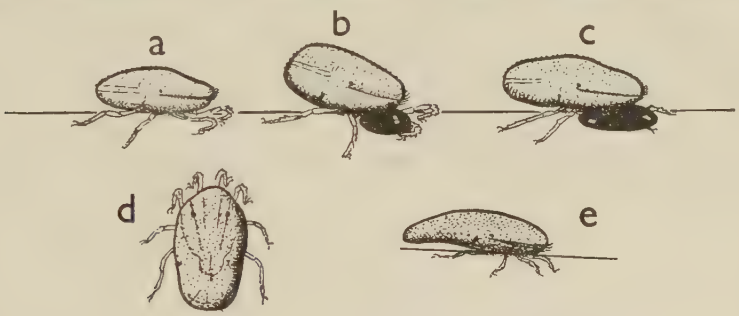

Fig. 2.—*O. moubata*, sketches of the shape of the South African strain: (*a*) during the first seven minutes of feeding; (*b*) at maximum engorgement; (*c*) during the last five minutes of feeding; (*d*) in dorsal view at maximum engorgement; (*e*) in lateral view the day after engorgement.

While two females from Jackales and four from Kokojane were typical in appearance when tested, feeding time was slightly longer than average and coxal fluid was delayed in appearance for a mean of 7·3 minutes.

In the last section it was shown that a low number of nymph stages was an absolute common factor to all the S. African *O. moubata* tested and held true over a vast distributional area. In this section certain less reliable characters are also shown to be common to all strains tested. These are the typical appearance during feeding, the lack of frontal contractions, the occurrence of unilateral secretion of coxal fluid and the delay in its appearance.

In this series of fifty females of Form E the mean feeding time was 37 minutes, coxal fluid was excreted for 68 per cent. of that time with a delay in its first appearance of 11 minutes. The corresponding figures for the East African forms was 25 minutes, 82 per cent. and 5 minutes in Form A: 49 minutes, 86 per cent. and 7 minutes in Form B: 29 minutes, 59 per cent. and 17 minutes

in the wild Form C. These data were obtained from pure cultures subsequent to observations given in Walton (1958*b*) and include the period of slow feeding at the end of a meal in Form B. Males of Form E from Angola and Lehututu agree closely with the females, but a striking difference occurs between the males of Form E and Form C, which they tend to resemble in appearance during feeding. Whereas males of Form C require a mean of 12 minutes to complete a meal, Form E males required 33 minutes.

4. Mode of Hatching

Another characteristic of the Groot Marico, Lehututu and Nova Lisboa strains was noted in the mode of hatching. Whereas the eggs of East African

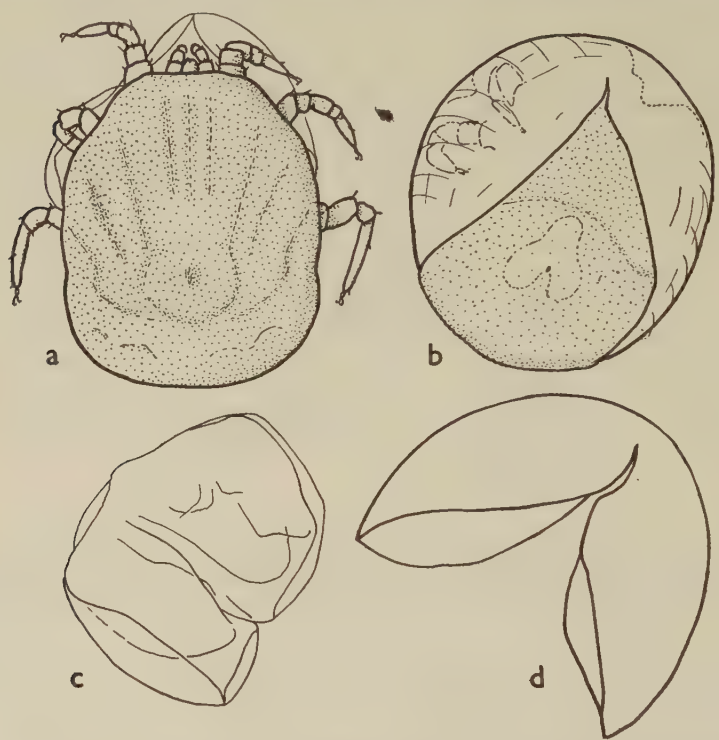

Fig. 3.—*O. moubata :* (*a*) larva of the South African form after splitting the egg shell (it remains in this state for about five days before the nymph emerges from the larval skin); (*b*) larva of the East African forms after splitting the egg shell (it remains in this position for about seven days until the nymph emerges from the larval skin and egg shell); (*c–d*) typical shape of the discarded egg shell of: (*c*) South African form; (*d*) East African forms.

strains, both wild and domestic, almost invariably split to expose a completely inactive larva which remains inactive for seven days firmly wedged between the two halves of the egg shell with its legs tightly folded until the nymph finally emerges from the larval skin and egg shell in one action, the larva of the Groot Marico, Lehututu and Nova Lisboa strains is semi-active and the majority

succeed in escaping completely from the egg shell, which usually becomes crumpled and adheres to the underside of the larva where its presence is easily overlooked (fig. 3). Having achieved this position the six-legged larva then becomes quiescent until the eight-legged nymph emerges from the larval skin. This period is about four days. The egg shell of the South African strains is so transparent and soft that the larvae could be easily mistaken for nymphs on casual inspection. The legs of these larvae are, however, shorter than the eight legs of the nymph and the body surface is much smoother.

In the Groot Marico and Lehututu strains the period from oviposition to the first appearance of the split in the egg shell averaged ten days, and the nymph emerges after a further six. In the Angolan strain from Nova Lisboa both periods occupied five days each, and this difference is correlated with an increase in the period between copulation and egg laying. In the Groot Marico and Lehututu strains this period varies from ten to thirteen days but was 16 in nine females of the Angola strain.

5. Other Details of Life History

Since a high proportion of the South African strains mature after three or four nymph stages, many of the males and females are of small size. Males may be only 4 mm. long and 3 mm. wide, and females only 5 mm. long and 3·7 mm. wide, but individuals of both sexes derived from the fourth and fifth nymph stages are no smaller than individuals of the East African strains.

These unusually small *O. moubata* have proved to be far more resistant to desiccation than any of the wild or domestic East African strains (*in the press*) but their resistance to prolonged starvation has not been studied as has that of the East African strains (Walton, 1957 and 1958*b*).

Eggs are light brown and oval in shape when laid, 0·980 mm. long, and darken as they mature. The mean weight of eggs of the Groot Marico strain was 0·352 mgm. and 0·448 mgm. in the Lehututu strain. The mean number of eggs laid in the first egg batch by ten females (random sample) of the Groot Marico strain was 313 (range 253–458) and was 200 (range 126–328) in the Lehututu strain. Nine females of the Nova Lisboa strain laid a mean number of 196 eggs (range 138–249). Thus the Groot Marico strain laid as many eggs as the East African Form A strains (Walton, 1958*b*), while the Lehututu and Nova Lisboa strains produced roughly the same number of eggs as the East African females of Forms B and C (Walton, 1958*b*). The eggs of the Lehututu strain were relatively larger (mean length of 48 eggs 1·028 mm.) than the eggs laid by either the Groot Marico strain (mean length of 44 eggs 0·962 mm.) or the Angolan strain (mean length of 50 eggs 0·952 mm.). The Lehututu females were, on the mean, somewhat larger than the females of the other strains (mean length of 20 Lehututu and Groot Marico females 7·14 mm. and 6·48 mm. and mean width 5·15 mm. and 4·69 mm. respectively).

In the South African strains studied (Runta, Ramaquabane, Kokojane and Jackales) the period from copulation of the female parents to the emergence of the last females of the next generation was 93 days, whereas the similar periods for the East African domestic Form A Meru strain and the wild Form C Naivasha strain were 142 and 162 days respectively. The actual period spent in the nymph stage, after subtracting the periods required between

the dates of moulting of the nymphs and the dates of the first acceptance of a blood meal was 61 days in the South African strains, 92 days in Form A Meru strain and 97 days in Form C Naivasha strain.

There was no appreciable difference in the length of the first four nymph stages in any of the *O. moubata* strains studied, which were 8 to 9 days, 7 days, 9·5 to 11 days and 9 to 10 days respectively.

The South African domestic strains are capable of producing a new fertile generation in just over 70 days as compared to 100 days in the East African domestic strains.

6. Discussion

The available evidence indicates the existence of a distinct biological variant of *O. moubata* inhabiting native dwellings over a wide area of the dry central highland plateau of South Africa, where the rainfall is low and unreliable, the relative humidity is liable to marked variation, and the mean temperature is low in comparison to the dry but hot habitat of Form D in central Tanganyika in East Africa (Walton, 1958*a* and *b*).

This variant does not seem to be able to exist in the extreme south, possibly because the mean temperatures are too low. The 70° F. isotherm appears to be the limiting factor (fig. 1). The rainfall at Runta and Groot Marico is approximately 30 inches per annum, but this figure is derived from a number of consecutive years of low rainfall and very low humidities followed by one with exceptionally heavy falls of short duration. Only drought-resistant organisms can survive under such conditions and this variant of *O. moubata* has been shown by us to fulfil these requirements (information on desiccation to be published separately). The Lehututu strain was obtained in the centre of the Kalahari desert and the Kokojane strain from its edge. The Lehututu strain may be partly adapted to such an environment by producing slightly larger eggs than the other strains studied and by simply being larger.

The Runta strain from the Okovanggo area in the extreme north-east of South West Africa on the Angola border seems to resemble the Transvaal and Bechuanaland strains very closely, but the Windhoek and Nova Lisboa strains from central South West Africa and Angola appear to be slightly aberrant, and this may indicate the existence of a north-western variation within the main distribution of the variant itself, as might be expected over so large a distributional area. Nova Lisboa is situated at an altitude of 5000 feet and receives a mean annual rainfall of 47 inches. This situation might appear unsuitable to a form of *O. moubata* obviously adapted to live in more arid conditions, but its occurrence there could be accounted for by transport distribution, since Nova Lisboa is a capital town and is connected to the arid Atlantic littoral by railroad.

Ramaquabane is situated on the railway line only sixty miles south-west of Bulawayo and Jackales is just north of Ramaquabane near the border of Southern Rhodesia. According to Zumpt (1958) *O. moubata* is uncommon in this area, but he clearly indicates the difficulty of finding these ticks in native huts in which they may in reality be quite abundant (*see* Ordman, 1941, who also comments on this point). This variant may therefore be expected to occur in Southern Rhodesia with the distinct possibility that it will be found in the south of Northern Rhodesia. Dr. F. Zumpt is at present engaged on

a study of the epidemiology of relapsing fever in Bechuanaland and will be reporting on the food requirements of this variant at a later date. In this connection it is apparent that relapsing fever is rare in those parts of South Africa where this tick is known to be abundant.

A comprehensive study of the morphology of this variant, together with five East African forms, is now being undertaken by the author. Further collections of living *O. moubata* are being sought from areas lying between East Africa, S. Rhodesia and Angola in an attempt to define the ultimate distribution of the various biological forms, and it is hoped that some means of immediate recognition may be achieved in the near future to replace the tedious biological approach. In the meantime, this variant from the South African area is being referred to as *O. moubata* Form E.

7. Summary

1. Evidence is given for the existence of a distinct South African domestic form of *Ornithodoros moubata* Murray designated Form E.

2. This Form E differs from all East African forms (A, B, C and D) by its paler more slender legs, smaller average size, light grey colour and in having a shorter life cycle.

3. It differs from all East African forms except the wild " warthog-burrow " Form C by assuming a semi-spherical and tightly distended shape in the middle of a feed and by the almost complete lack of frontal contractions usually associated with the secretion of coxal fluid.

4. This coxal fluid appears later during a feed than in the East African domestic forms, but appears earlier than it does in the wild " warthog burrow " strains.

5. In Form E the majority of the males reach maturity after three nymph stages and none requires five stages. Among the females the majority reach maturity after four feeds and less than 1 per cent. require five feeds, whereas no females of the East African strains have ever reached maturity with less than four feeds.

6. Whereas in the East African forms emergence from the egg is delayed until the larval moult has occurred, in Form E it is the semi-active larva which hatches and it then becomes inactive until the larval moult occurs. On hatching the egg shell usually becomes crumpled beneath the larva in Form E, completely exposing it to view, whereas in all East African forms the larva remains inactive and wedged inside the cracked egg until the nymph emerges from the egg and larval skin in one act.

7. Form E is adapted to withstand severe desiccation and its distribution extends over Bechuanaland, Western Transvaal, South West Africa and Angola, and includes the Kalahari Desert. The 70° F. isotherm appears to be the limit of its southern distribution. It therefore inhabits cool and dry country as distinct from the hot and dry country inhabited by Form D, the cool and wet country inhabited by Form A and the hot and moist conditions inhabited by Form B.

8. Form E has rarely been found to be infected by *Spirochaeta duttoni*, and may therefore be an inefficient vector of human relapsing fever.

8. Acknowledgments

I wish to thank Dr. Botha de Meillon for the gift of the Groot Marico strain, Dr. Vasco Antunes Sousa Dias for kindly supplying the Nova Lisboa strain and Dr. F. Zumpt for so kindly sending me the strains of *O. moubata* from Lehututu, Ramaquabane, Kokojane, Jackales, Runta and Windhoek and for information concerning the climate of the localities. Special recognition is deserved by Mr. K. L. Cockings who made the observations on the number of nymph stages when working as Technical Assistant.

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Appendix

The number and percentage of feeds and nymph stages required to reach maturity by both sexes of the Lehututu, Ramaquabane, Kokojane, Jackales, Windhoek and Runta strains of South African O. moubata

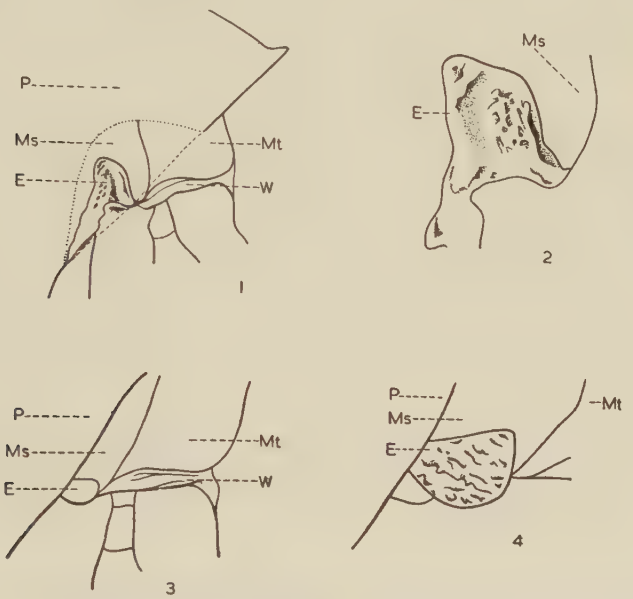
		Number					%				
No. of feeds		3	4	5	6	7	3	4	5	6	7
Lehututu, Bechuanaland	♂	142	3	0	0	0	98	2	0	0	0
	♀	35	102	0	0	0	25·5	74·5	0	0	0
	Total	177	105	0	0	0	63	37	0	0	0
Ramaquabane, Bechuanaland	♂	79	30	0	0	0	72·5	27·5	0	0	0
	♀	0	122	3	0	0	0	97·6	2·4	0	0
	Total	79	152	3	0	0	33·7	64·9	1·3	0	0
Kokojane, Bechuanaland	♂	137	3	0	0	0	97·8	2·1	0	0	0
	♀	4	108	0	0	0	3·6	96·4	0	0	0
	Total	141	111	0	0	0	56	44	0	0	0
Jackales, Bechuanaland	♂	96	9	0	0	0	91·4	8·6	0	0	0
	♀	19	83	1	0	0	18·4	80·6	0·9	0	0
	Total	115	92	1	0	0	55·3	44·2	0·5	0	0
Windhoek, S.W. Africa	♂	46	15	0	0	0	75·4	24·6	0	0	0
	♀	1	65	0	0	0	1·5	98·5	0	0	0
	Total	47	80	0	0	0	37·0	62·9	0	0	0
Runta, S.W. Africa	♂	110	7	0	0	0	94·0	5·9	0	0	0
	♀	0	143	0	0	0	0	100	0	0	0
	Total	110	150	0	0	0	42·3	57·7	0	0	0

PRESENCE OF ELYTRA IN SUPPOSEDLY APTEROUS GENERA OF THE FAMILY PAMPHAGIDAE (ACRIDOIDEA, ORTHOPTERA)

By Joyce B. Mason

(*Anti-Locust Research Centre*)

Certain genera in the family Pamphagidae have always been considered as completely apterous but a close examination has shown that they have vestigial elytra. The genera examined are *Tropidauchen* (11 species, 103 specimens),

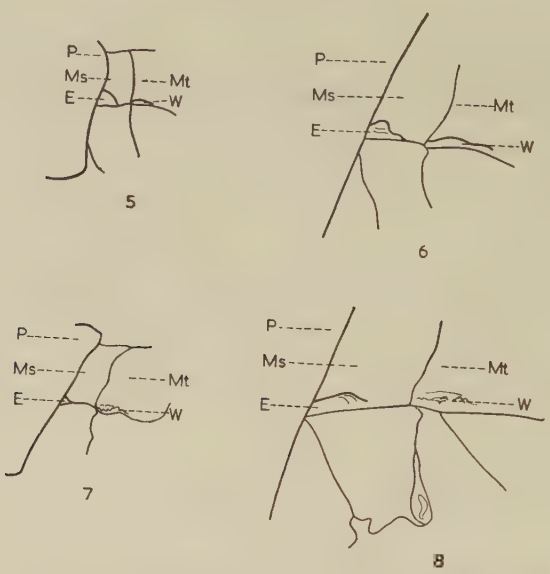


Figs. 1–4.—*Tropidauchen marginatum* I. Bol.: (1) male elytron in upright position under pronotum. A part of the posterior margin of the pronotum has been excised along the dotted line, the normal posterior margin being represented by a broken line; (2) ditto, larger magnification; (3) female elytron, normal horizontal position; (4) ditto, larger magnification. *P*, pronotum; *Ms*, mesonotum; *Mt*, metanotum; *E*, elytron; *W*, wing.

Nocarodes (13 species and subspecies, 74 specimens) and *Nocaracris* (2 species, 13 specimens). The elytron development in these genera varies from just a small fold of integument to a vestigial elytron, without definite venation. The wing is absent but may be represented by a small ridge.

The most developed elytra are found in *Tropidauchen marginatum* I. Bolivar, 1912, in which a female elytron is 1·8 mm. and a male elytron 2·3 mm. long. These small elytra are often hidden beneath the pronotum and the insect

appears apterous until the pronotum is excised (figs. 1, 2). In many cases a vestigial hind wing, represented by only a small ridge or fold of integument, is also present on the metanotum. In *T. marginatum* the elytra are sometimes in an upright position (figs. 1, 2) and sometimes in the normal (figs. 3, 4). Different development may even be found on the two sides of the same insect, which may have a vestigial elytron on one side only. Amongst 13 males examined, three have elytra in the normal position, including one on one side only; in the other ten males, vestigial elytra are under the pronotum. Amongst 18 females, six have elytra in the normal position, including three with elytra



Figs. 5–8).—(5, 6) *Nocaracris rubripes* (F. W.): (5) male elytron partly hidden by pronotum; (6) female elytron partly hidden by pronotum. (7, 8): *Nocarodes serricollis* (F. W.): (7) male elytron partly hidden by pronotum; (8) female elytron partly hidden by pronotum. (For explanation of lettering *see* figs. 1–4.)

only visible on one side; the other 12 have vestigial elytra hidden under the pronotum.

In all other species of *Tropidauchen* small elytra are found in an upright position, wholly or partly hidden by the pronotum.

In *Nocaracris* minute vestigial elytra are also present and partly hidden beneath the pronotum. The wing is absent, but sometimes a slight ridge may be seen on the metanotum (figs. 5, 6).

In *Nocarodes* (figs. 7, 8) all species have vestigial elytra under the pronotum in an upright position. The exposed portion of the elytra varies within the individuals and even on two sides of the same specimen. The female often appears to have more of the elytra exposed, but this is probably due to the size of the abdomen and the degree to which the pronotum covers the meso- and metanotum.

Conclusion

The fact that these three genera are not completely apterous, as previously thought, but possess vestigial elytra in different stages of reduction, suggests that they have lost the use of their elytra and wings relatively recently.

Acknowledgment

I wish to express my gratitude to Dr. B. P. Uvarov for suggesting the work and for his advice.

Book Notices

The Diptera of Lancashire and Cheshire. Pt. 1. By L. N. Kidd and A. Brindle. 8vo. Arbroath (Lancashire & Cheshire Fauna Committee), 1959. Pp. 136. 21s.

This list has been compiled by a sub-Committee of the Lancashire and Cheshire Fauna Committee.

Most of the information on this region is widely scattered, and the list is to be divided into four sections of which two, Nematocera by L. N. Kidd, Brachycera and Cyclorrhapha by A. Brindle, are included in Part I. A bibliography is included and a supplementary one will be published with the two final sections.

The nomenclature follows Kloet and Hincks' *Check List*, and under each species information is given on the flight period of adults, distribution, degree of frequency, and on the habitat of adults and/or immature stages.

The Odonata of Canada and Alaska. Vol. 2, Pt. III: *The Anisoptera—four families.* By Edmund M. Walker. 8vo. Toronto (University Press), 1958; London (Oxford University Press), 1959. Pp. xi, 318, 64 pls. 105s.

This volume deals with the families Aeshnidae, Petaluridae, Gomphidae and Cordulegastridae. There is a section on the general characteristics of Anisoptera, followed by keys to families, genera and species, with information on taxonomy; habitat and range; distribution; and field notes. The work is very fully illustrated. All the drawings, with the exception of a few from photographs by Wm. Carrick, are by the author.

The remaining families of Macromiidae, Corduliidae and Libellulidae will be described in Volume 3.

THE RETROCEREBRAL COMPLEX AND VENTRAL GLANDS OF THE PRIMITIVE ORTHOPTEROID *GRYLLOBLATTA CAMPODEIFORMIS* WALKER, WITH A NOTE ON THE HOMOLOGY OF THE MUSCLE CORE OF THE "PROTHORACIC GLAND" IN DICTYOPTERA

By C. A. Rae and A. F. O'Farrell

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Introduction

Both prothoracic and ventral glands (or "head lobes") are present in the cockroach *Blattella germanica* (L.) (Rae, 1955), but other orthopteroid insects so far studied, including Blattids, appear to possess one or the other, but not both (Chadwick, 1955 and 1956; Pflugfelder, 1947; Rae, 1957; Scharrer, 1948). The situation in *Grylloblatta campodeiformis* Walker, described as a "living fossil" (Walker, 1937), thus seemed worth investigation. Moreover, the retrocerebral complex of this insect has not so far been described, either in the special studies of Walker (1931, 1933, 1938, 1943, 1949) or in the general treatise of Cazal (1948). The present investigation was made possible through the kindness of members of the Canadian Science Service, notably Dr. Holland, in providing material from the exhibit of living *G. campodeiformis* staged at the Tenth International Congress of Entomology in Montreal.

Materials and Methods

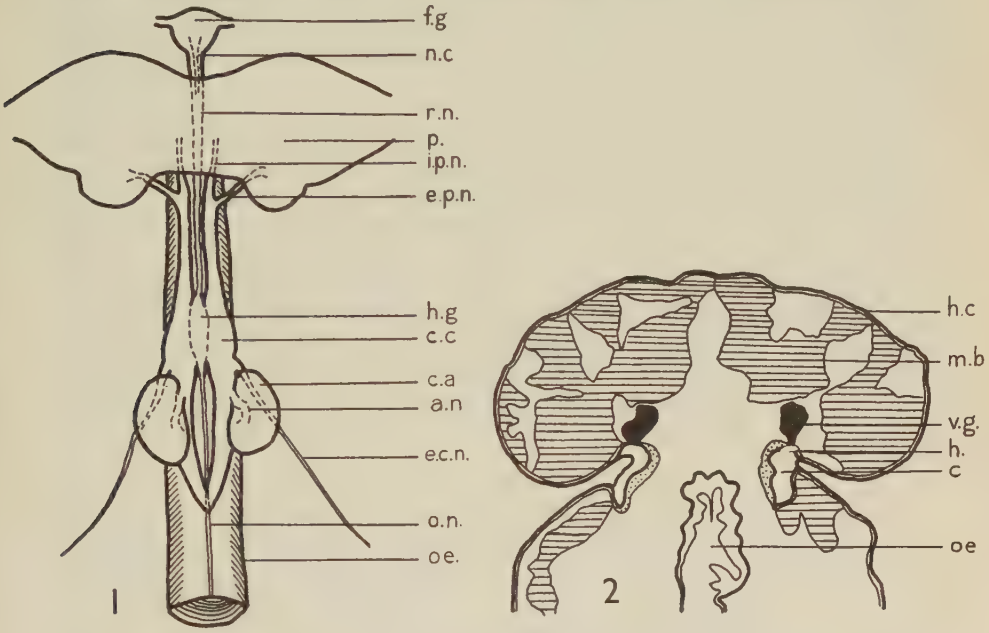
Two adult males, three medium-sized (? fifth or sixth instar) nymphs and two smaller (? second instar) nymphs were studied. The specimens were cut through the mesothorax and fixed in Carnoy's fluid (three specimens), alcoholic Bouin (two specimens) or aqueous Bouin (two specimens). Sections of the entire head and prothorax were cut at 5, 7 or 10 μ, according to size and hardness of the specimen. The Carnoy series (one of each stage available) was stained with haematoxylin and eosin for general topographical study. The alcoholic Bouin series (one adult male, one medium nymph) was stained with Azan, for comparison with similarly treated material of *Blattella germanica* available in the laboratory. The aqueous Bouin series (one small and one medium nymph) was stained with Gomori's (1941) chrome-haematoxylin/phloxin, to demonstrate neurosecretory material. The following account is based upon examination of these three series.

Results

Anatomy and Histology of the Retrocerebral Complex

The general topography of the complex is shown in figure 1 and (so far as it is traceable from a single section) in Plate I, *A*. A very fine and tenuous nervus connectivus connects the protocerebrum with the well-developed frontal ganglion, from which an unpaired recurrent nerve runs back along the oesophagus into the hypocerebral ganglion and thence, as the oesophageal nerve,

to the stomodaeal ganglion figured by Walker (1949). There is a distinct and well-defined hypocerebral ganglion, lying behind the brain in the angle formed between the anterior ends of the corpora cardiaca. The ganglion is slightly tapered anteriorly and posteriorly, and shows a markedly peripheral arrangement of the ganglionic cells (Plate I, *B*). There is close contiguity and apparently an exchange of nerve fibres between the hypocerebral ganglion and the corpora cardiaca over a region extending from about half to about five-eighths of the way along the anteroposterior length of the latter.



Figs. 1–2.—*Grylloblatta campodeiformis*. Diagrammatic representation of (1) the retrocerebral complex ; (2) the position of the ventral glands. (For explanation of lettering see p. 82).

The corpora cardiaca are paired swellings in the aortic wall. They are greatly elongated, somewhat ribbon-like structures, fairly uniform in width and thickness, without local swellings or bulges ; they are fused together for about one-eighth of their total length in their ventroposterior regions. Each corpus cardiacum is innervated from the protocerebrum by a large internal cardiacal nerve and a very thin external cardiacal nerve ; these nerves run a comparatively long extra-cerebral course before entering the corpus cardiacum at its anterior end. In addition, a very tenuous nerve can be traced from each corpus cardiacum, running along the surface of the oesophagus and vanishing among the muscles near the tentorium. Histologically, the corpus cardiacum consists of a central region with sparse nuclei, apparently consisting mainly of nervous elements ; the peripheral portion, however, contains numerous nuclei of characteristic appearance. They are spherical to ovoid in shape, with the chromatin localised into small areas giving the nucleus a

" dotted " appearance—a feature of the nuclei in the retrocerebral organs of many insects. A well-defined connective tissue sheath, staining bright blue with Azan, invests the corpora cardiaca.

(In sections from the nymphs fixed in aqueous Bouin, the Gomori stain revealed densely packed neurosecretory material, staining a deep blue-black, filling the intercellular spaces of the corpora cardiaca. No such material was visible in the internal or external cardiacal nerves, or near their origins in the brain ; and no neurosecretory cells were demonstrated in the brain or sub-oesophageal ganglion. Such cells are often difficult to observe, *e.g.* in *Blattella germanica* they are seldom clearly recognisable although undoubtedly present ; hence it is not surprising that they were not seen in the limited material of *Grylloblatta* available for study.)

The corpora allata are comparatively large, compact, paired bodies, of regular ovoid shape, lying almost symmetrically on either side of and in the same plane as the corpora cardiaca, just anterior to the posterior fused portion of the latter (Plate I, *C*). Each corpus allatum is about one-fourth the length of the corpus cardiacum, to the lateral border of which it is very closely applied. A very fine and short allatal nerve runs from the corpus cardiacum into the corpus allatum. A delicate connective tissue membrane invests each corpus allatum, which contains densely packed nuclei with " dotted " chromatin, usually surrounding a more or less defined central " fibrous " region in which nuclei are sparse or absent. Some mitotic figures were seen in the corpora allata of the young nymphs, and they were comparatively abundant in those of the adults.

Anatomy and Histology of the Ventral Glands

The ventral glands are large paired organs in the ventro-caudal region of the head, lying in the same plane as the retrocerebral complex. Topographically, they correspond in position to the " head lobes " of *Blattella germanica*, (Rae, 1955) and in general they resemble the ventral glands of the lower Pterygota as described by Pflugfelder (1947).

The structure and histological appearance of the ventral glands undergo considerable changes during development. In the young nymphs, the glands are small stalked vesicles, attached to the hypodermis near the tentorial pit invaginations, and extending forward into the head capsule (fig. 2). In older nymphs, they are relatively as well as absolutely larger in size, extending backward into the neck as well as forward into the head capsule, occupying the space between the tentorial pit invaginations and the large longitudinal tracheal trunks lying on either side of the oesophagus ; they retain a stalk-like connection with the hypodermis and have a somewhat lobulated appearance (Plate I, *D*). The ventral glands of the adult males are large and massive, with cushion-like bases formed by thickening of their attachments to the hypodermis. One of the two specimens studied had the glands strongly asymmetrical, that on one side being many times larger than the other (Plate I, *E*). No nerve supply to the ventral glands was detected in any of the specimens.

In all stages, each ventral gland is surrounded by a very delicate connective tissue sheath, staining blue with Azan. Within this are closely packed numerous very large nuclei, mostly more or less spherical but graduating towards ellipsoidal in shape, and having large prominent nucleoli. The

chromatin is again so distributed as to give the nuclei a dotted appearance. Some intercellular spaces are present in most specimens; usually devoid of visible contents in nymphs, these spaces are more numerous in the adult males and sometimes contain what appear to be products of cytoplasmic breakdown. In the male with asymmetrical glands, the larger gland contained one extensive cavity which had within it a large bolus of material staining deep blue-black with haematoxylin (Plate I, *F*). The glands of both adults contained many pycnotic nuclei, suggesting that a process of degeneration had begun. In one of the two young nymphs, fixed in alcoholic Bouin and stained with Azan, the central regions of both glands were devoid of nuclei and contained droplets, presumably of secretory origin, staining bright blue. Similarly staining cellular inclusions, not droplets, have been observed in the corpora allata of *Gryllotalpa* by Palm (1947) and of *Blattella* (Rae, *unpublished*), but their significance remains uncertain.

A short distance behind the hypodermal origins of the ventral glands are the anterior insertions of the paired " coxal muscles of the first cervical sclerite " (No. 49 of Walker (1938)). In *Grylloblatta* these muscles are relatively large and conspicuous. They cross over one another and follow a general course which strongly suggests that they are identical with the fine strands of muscle forming the cores of the X-shaped prothoracic glands of Blattids (Bodenstein, 1953; Rae, 1955; Scharrer, 1948). No extensive or conspicuous glandular tissue appears to be associated with these muscles in the *Grylloblatta* material examined, although one specimen has an isolated group of three or four cells resembling ventral gland tissue just anterior to the crossing over of the muscles.

Discussion

As shown in Table I, the retrocerebral complex and ventral glands of *Grylloblatta* display a fairly generalised orthopteroid condition, as might be expected in such a primitive insect.

There seems to be a particularly close resemblance between the Grylloblattids, the Isoptera and the more primitive members of the Orthoptera Ensifera.

The resemblance to the Orthoptera Coelifera, Cheleutoptera and Dictyoptera, although still obvious, is less marked. Resemblances to other Orthopteroid orders appear distinctly more remote. The general indications derived from Table I seem to conform reasonably well with the schemes of Grylloblattid relationships put forward on different grounds by other workers; *e.g.* Caudell (1927); Crampton (1933); Walker (1933, 1938, 1949).

Despite the peculiarities of its habitat and life-history, it would be surprising if *Grylloblatta* showed fundamental differences from other Orthopteroids in the general functions of its retrocerebral complex and ventral glands. Direct experimental evidence is not available, and the material examined histologically in the present investigation was limited in quantity and uncertain in age. Nevertheless, obvious storage of Gomori-positive material in the corpora cardiaca of the nymphs, together with the observed changes in the ventral glands, including signs of degeneration in the adult, suggest that the functions of these organs in *Grylloblatta* may closely resemble those observed in better-known insects.

TABLE I.—*Comparison of seven major anatomical features of the retrocerebral complex and ventral glands in Orthopteroid insects, compiled from the work of Cazal* (1948), *Pflugfelder* (1947) *and Rae* (1955, 1957 *and unpublished*).

	Condition in							
Anatomical feature	*Grylloblatta campodeiformis*	Isoptera	Orthoptera	Dictyoptera	Cheleutoptera	Plecoptera	Dermaptera	Embioptera
Nervus connectivus present	+	+	−	+	−	?	−	+
Hypocerebral ganglion conspicuous	+	+	+	±(1)	+	+	+	−
Oesophageal nerve unpaired	+	+	±(2)	+	+	±(3)	−	+
Corpora allata paired	+	+	+	+	+	±(3)	−	−
Corpora cardiaca ribbon-like	+	−	±(4)	−	−	−	−	−
Ventral glands cephalic	+	+	+	±(5)	+	+	+	?
" Prothoracic glands " present	−	−	−	+	−	−	−	?

(1) Less conspicuous than in other Orders, but much more so than in Embioptera.
(2) *Tachycines* appears to be the only genus of Orthoptera known to show the unpaired condition.
(3) Both paired and unpaired conditions are found within this order.
(4) Primitive Ensifera, e.g. *Gryllotalpa*, *Gryllus*, etc., alone have ribbon-like condition.
(5) Cephalic ventral glands are usually absent.

The unsuccessful search for organs in *Grylloblatta* corresponding to the so-called " prothoracic glands " of Dictyoptera has thrown some light on the homologies of the muscular " cores " of the latter. In Blattids these muscle cores are very thin and difficult to trace ; thus they appear to have been overlooked in the standard account of the thoracic musculature of *Periplaneta* (Carbonell, 1947). A careful re-examination of the courses followed by the muscle cores of the " prothoracic glands " in Blattids suggests that they represent the remnants of the quite large muscles designated " cruciate rotators of the head " in *Gryllus* by du Porte (1920) and " coxal muscles of the first cervical sclerite " in *Grylloblatta* by Walker (1938). In the Mantid *Orthodera* (Rae, 1957), the muscle cores of the " prothoracic glands " are much more conspicuous than in Blattids, but their full course is not easy to trace because they tend to merge almost indistinguishably with other elements of the prothoracic musculature.

The Dictyoptera appear to be unique among the Orthopteroids in that they have these muscles invested with glandular tissue, apparently identical in appearance and function with the ventral glands. Whether these " prothoracic glands " are to be regarded as homologous with the apparently functionally similar prothoracic structures found in other insect orders seems open to doubt ; the use of the term " Scharrer's organ " (Chadwick, 1955) for the characteristic X-shaped " prothoracic gland " of Dictyoptera may thus be justified.

Summary

1. The retrocerebral complex and ventral glands of *Grylloblatta campodeiformis* Walker are described from material including nymphs and adult males.

2. A comparison of their condition in *Grylloblatta* with that seen in other Orthopteroids appears to support existing views on Grylloblattid relationships.

3. There is evidence of storage of neurosecretory material in the nymphal corpora cardiaca, and of degeneration of the ventral gland in the adult male.

4. " Prothoracic glands " are absent, but the coxal muscles of the first cervical sclerite appear to be homologous with the very slender muscle cores of the " prothoracic glands " of Dictyoptera.

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Explanation of Lettering

an, allatal nerve.
br, brain.
c, cuticle.
ca, corpus allatum.
cc, corpus cardiacum.
ecn, external collateral nerve.
epn, external paracardiacal nerve.
fg, frontal ganglion.
h, hypodermis.
hc, head capsule.
hg, hypocerebral ganglion.
ipn, internal paracardiacal nerve.
mb, muscle block.
nc, nervus connectivus.
oe, oesophagus.
on, oesophageal nerve.
p, protocerebrum.
rn, recurrent nerve.
vg, ventral gland.

PLATE I

Grylloblatta campodeiformis Walker

Horizontal sections of Carnoy-fixed material, cut at 7 μ and 10 μ and stained with haematoxylin and eosin, of the retrocerebral complex and ventral glands.

A. General view of complex in adult male, showing long ribbon-like corpora cardiaca and compact corpora allata.

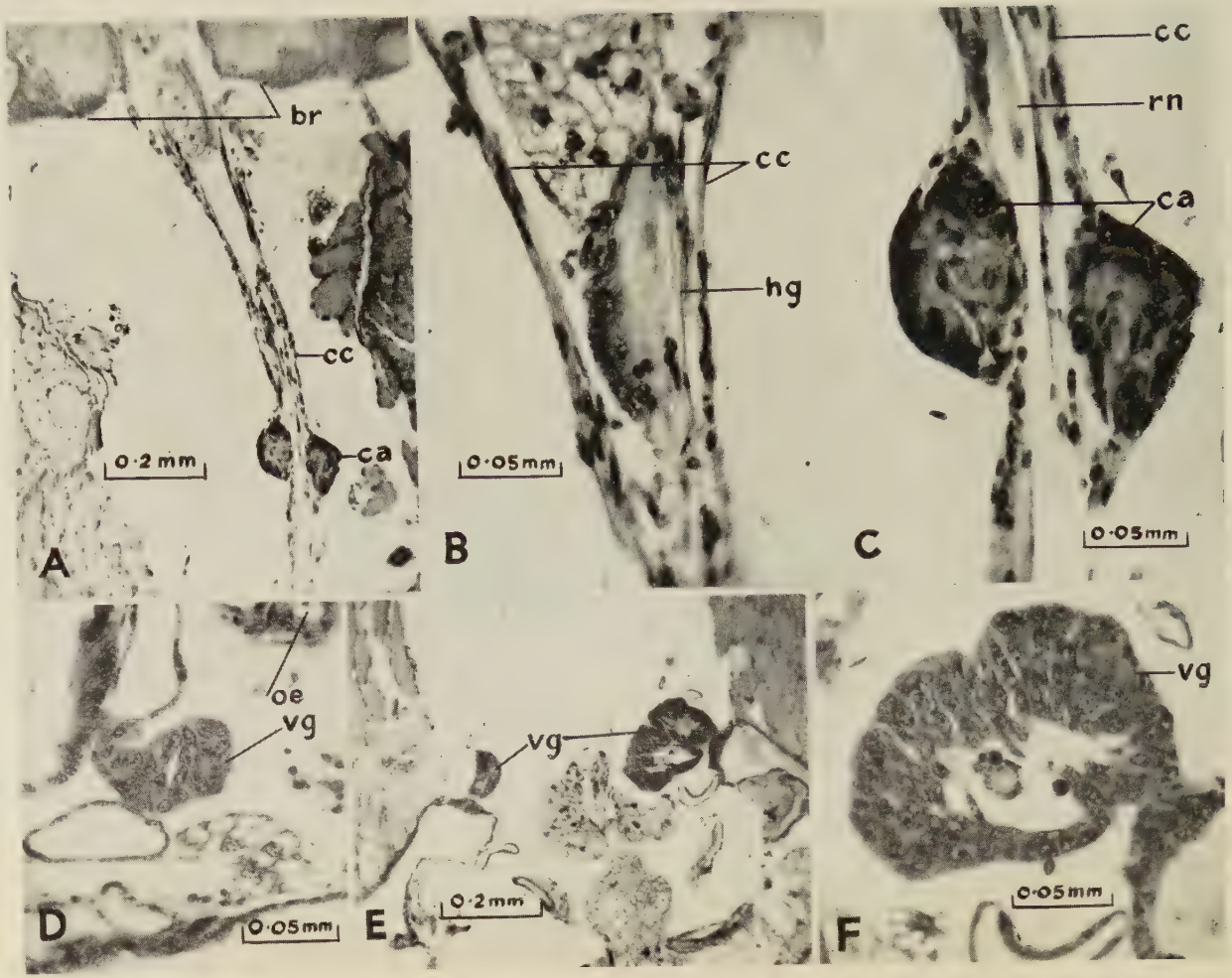
B. Hypocerebral ganglion lying between anterior portions of ribbon-like corpora cardiaca. Adult male.

C. Corpora allata of adult male, showing attachment to corpora cardiaca, peripheral distribution of nuclei and characteristic appearance of cytoplasmic core.

D. Ventral gland of medium-sized nymph.

E. Asymmetrical reduction in size of degenerating ventral glands in adult male.

F. Degenerative changes in ventral gland of adult male.



Grylloblatta campodeiformis Walker.

LARVAE OF THE BRITISH TRICHOPTERA—THE BERAEIDAE

By N. E. Hickin

(*Home Farm, Fetcham, Leatherhead, Surrey*)

The trichopterous family Beraeidae appears to have a fairly scattered world distribution but the number of genera and species is small. Kimmins gives two genera involving but three species in the Australasian region. Three species, all in the genus *Beraea*, are found in North America although confined to the eastern part. They occur throughout the Palaearctic region with the exception of Manchuria and Japan, and are present in the African region but absent from the whole of the Oriental region. This family is usually placed between the Sericostomatidae and the Molannidae.

The Beraeidae are represented in the British fauna by four species contained in three genera, as follows: *Beraeodes minuta* (L.), *Beraea maurus* Curtis, *B. pullata* Curtis and *Ernodes articularis* Pictet. These are numbered 53 to 56 respectively in my collection.

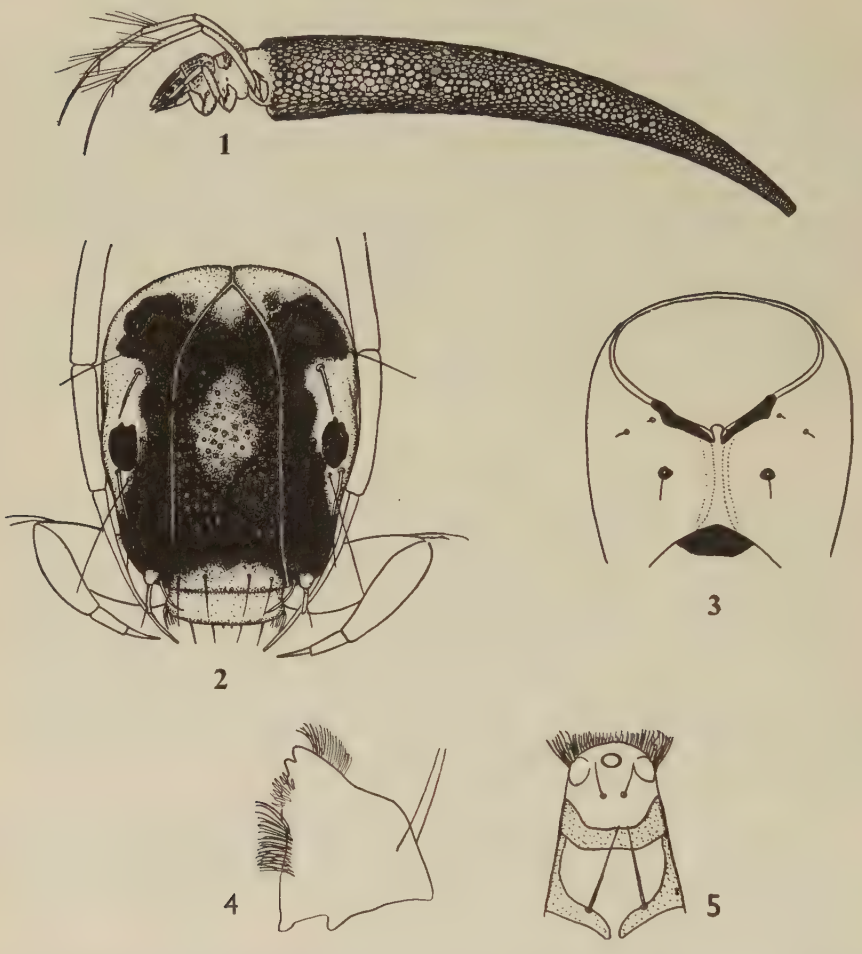
Beraeodes minuta (L.)

Larvae were collected on 17th April, 1955, from Toadsmoor, Gloucestershire, where they were present in very large numbers amongst the masses of underwater fibrous roots of willow trees under the banks near the outflow stream of the lake. I was visiting Toadsmoor with Mr. A. F. Peacey in search of the larvae of *Ernodes articularis* Pict., adults of which had previously been collected in this locality by Mr. Peacey, to whom I am greatly indebted for placing at my disposal his very wide knowledge of Gloucestershire insects. Adults of *Beraeodes minuta* commenced to emerge from my aquaria on 30th April, 1955 and continued to do so until 23rd May. Mr. D. E. Kimmins kindly confirmed the identification.

Case: conical, curved, up to 10 mm. long and 1·5 mm. wide, of very fine sand grains, the surface having a smooth appearance apparently due to a large proportion of silk-like secretion. *Larva:* 7–9 mm. long, 1·0–1·2 mm. wide; tarsal claws of prothoracic and mesothoracic legs normally held close to the mouthparts (fig. 2); metathoracic legs very long and slender, the tarsal claws being particularly slender.

Head (figs. 2, 3): clypeus and adjacent areas of genae mostly black; clypeus covered with fine hairs, each arising from a small white spot; edges of clypeus parallel until converging to the vertex; distal segment of antenna slender, bearing a bristle near the tip; genae apparently fused at mid-ventral line (it cannot be said for certain that any part of what I have in previous papers called the gular sclerite has taken part in this fusion). *Mandibles* (fig. 4): stout with three brushes of hair, the median brush being composed of shorter but stouter hairs. *Labium* (fig. 5): furnished with hairs at the tip, silk gland orifice large, basal lobe of labial palpi not differentiated. *Pronotum:* light golden-yellow with black reticulated pattern occupying anterior two-thirds, a fine hair arising from each reticulation; posterior third contains a few but larger black marks; mesonotum with a light brown partially sclerotised area with a few dark brown marks; prosternal horn absent. *Legs:* relative size shown

in figure 1, and shape of tarsal claws in figures 7, 8 and 9. *Abdomen :* bright apple green, gills present in small clusters from first to fifth segments ; lateral line absent but sclerotised tubercles present from third to eighth segment. *Anal claws :* basal segments slender with dark brown slender sclerite apparently articulating with distal segment ; claw bears two auxiliary claws (not shown in figure).



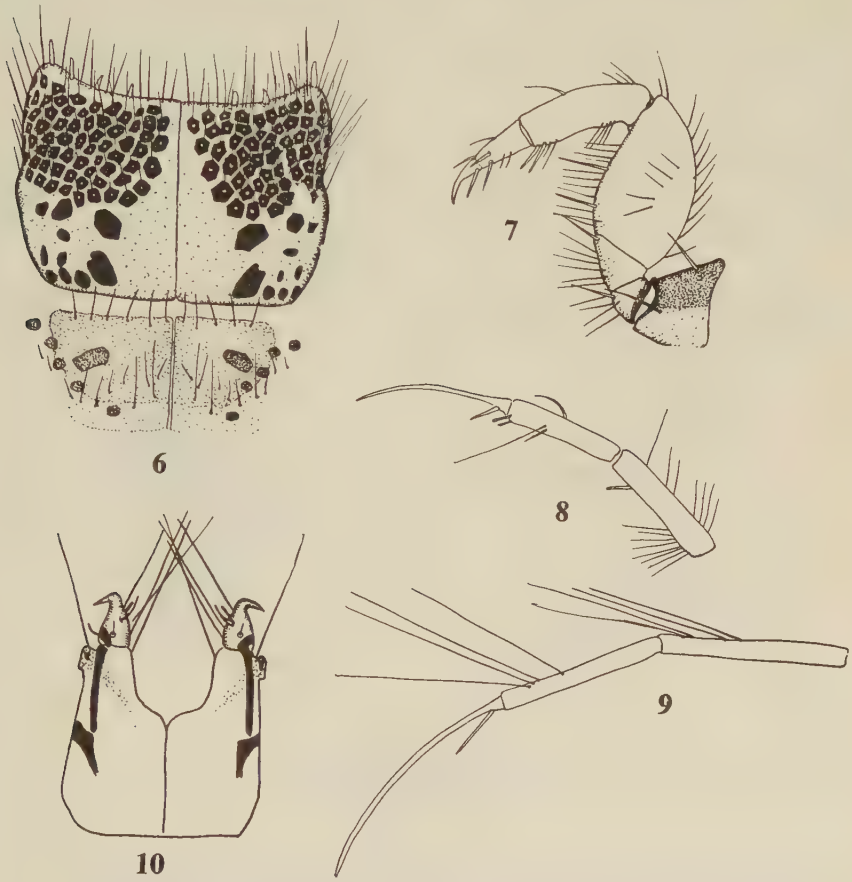
Figs. 1–5.—Larva of *Beraeodes minuta :* (1) Larva in case ; (2) head from the front, showing position of prothoracic and mesothoracic legs ; (3) head from below ; (4) mandible ; (5) labium.

Ernodes articularis Pictet

In spite of the widest search for British examples of larvae of *Ernodes articularis* Pictet, I have been unsuccessful. Moseley stated that this species was very local in this country, though widely distributed in alpine regions on the Continent. Dr. Georg Ulmer has, however, been kind enough to send

me some German specimens. The figures and references to this species in this paper refer to these specimens.

The larva strongly resembles that of *Beraea maurus* but differs as follows: All bristles on front of head (fig. 22) light coloured; pronotum (fig. 23) with a wide light creamy-yellow anterior margin; central transverse triangular part dark reddish-brown covered with fine light-coloured hairs; posterior part light creamy-yellow and separated from central part by a straight dark well-marked ridge. Metathoracic tarsal claw shorter and stouter than in *Beraea* (less than half length of tarsal segment) (fig. 24). Anal lobes (fig. 25) narrow and with only a few small hairs and a single large black bristle (curved in my specimens); anal claw bears only a single auxiliary claw.

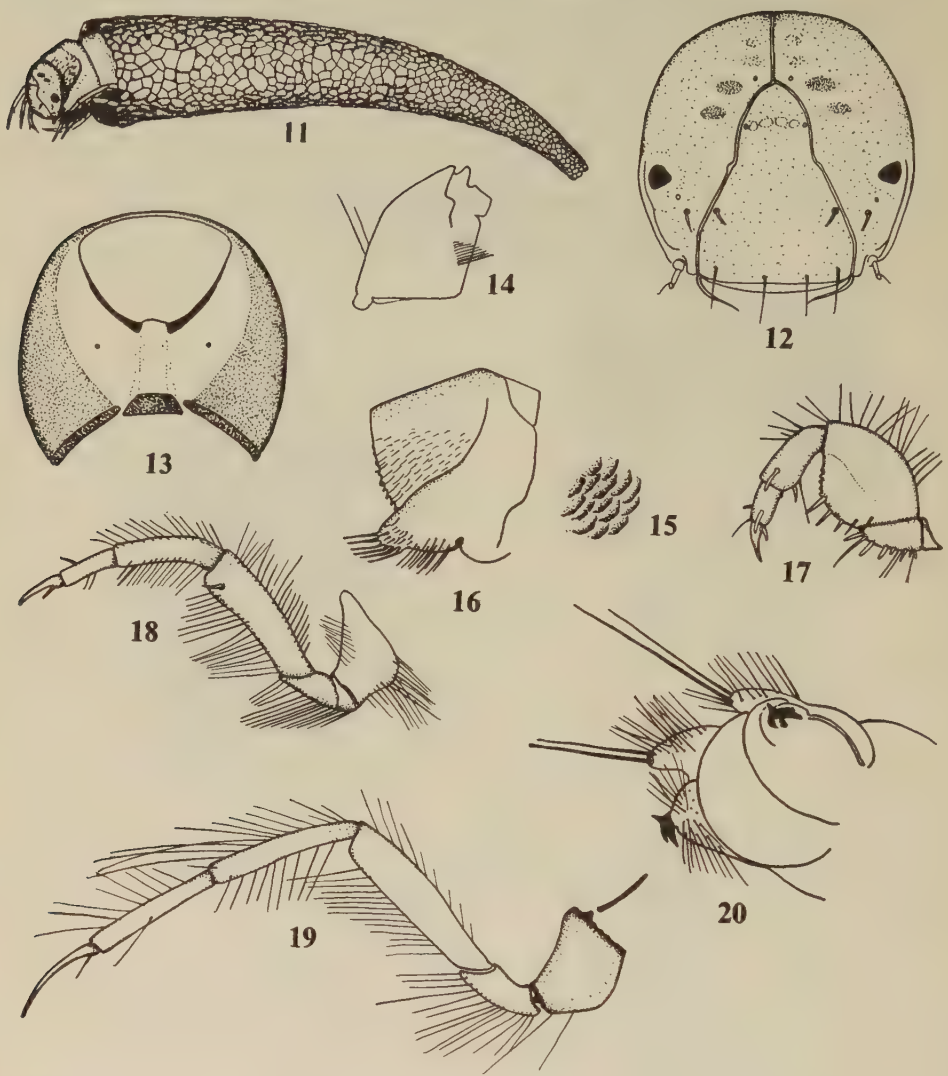


Figs. 6–10.—Larva of *Beraeodes minuta*: (6) Pro- and mesonota; (7) prothoracic leg; (8) tibia and tarsus of mesothoracic leg; (9) tibia and tarsus of metathoracic leg; (10) anal segment.

Beraea pullata Curtis

A number of larvae were collected from the derelict Thames-Severn Canal at Brimscombe, near Stroud, Glos., when I visited this locality with Mr. Peacey on 16th April, 1955. The larvae were found amongst the roots of the marginal

vegetation. An adult emerged from the aquarium on 15th May, 1955, and was identified by Mr. Kimmins. When freshly emerged the wings are violet-black.



Figs. 11–20.—Larva of *Beraea maurus:* (11) Larva in case; (12) head from the front; (13) head from behind; (14) left mandible; (15) " honeycomb " sculpturing of head; (16) pronotum from side; (17) prothoracic leg; (18) mesothoracic leg; (19) metathoracic leg; (20) anal segments partly from beneath.

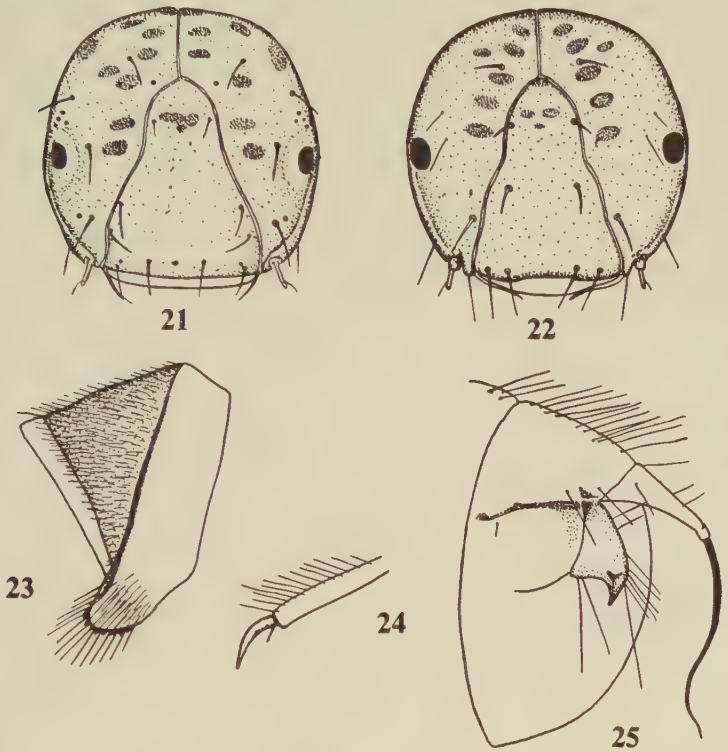
Nielsen (1942) has given a very detailed description of the larva of this species, with many figures, so that it is now proposed to deal with it only briefly.

Larva similar to that of *B. maurus*, but colour of head and pronotum slightly more orange; " muscle spots " on head more prominent and two brushes present on inside

edge of each mandible; the most distinctive differences, however, are the presence of only one large black bristle on each anal lobe, and of two brushes of hairs on the inner face of each mandible.

Beraea maurus Curtis

On 9th April, 1953, when collecting with Mr. Peacey at Cherrington, near Stroud, we found a larva of what I thought to be a Beraeid on a submerged branch in a small stream running into a lake, and on 24th May Mr. Peacey collected another dozen and sent them to me. Three specimens remained



Figs. 21–25.—(21) Larva of *Beraea pullata:* head from the front. (22–25) Larva of *Ernodes articularis:* (22) head from the front; (23) prothorax from the side; (24) metathoracic tarsus; (25) anal segments from the side.

alive in a small aquarium for a few weeks but did not survive. Then in February 1954 Mr. Peacey sent a further small batch from the same locality and from these two adults emerged, one on 19th June and the other on 25th June, 1954. Mr. Kimmins kindly identified them as *Beraea maurus* Curtis.

Case (fig. 11): length 7·0 mm., diameter at anterior end 1·1 mm., of small sand grains cemented together, curved and diminishing towards the hinder end; posterior end, although very small in transverse section, is further almost entirely filled in by a greyish secretion, to which a few minute grains of sand become attached, so that a small crescentic opening only remains. *Larva:* length 6 mm., width 0·9 mm., widest at about first

abdominal segment; head and pronotum bright brick-red. *Head* (fig. 12): round when seen from in front, covered with fine sculpturing (fig. 15); clypeus broad, almost triangular; a furrow just ventral to the eye runs to the antenna; antenna of three segments, basal one of which is not distinct, and a bristle arises at the base of the small distal segment; on ventral surface the genae appear to be united, the characteristic gular sclerite being absent as a discrete part (fig. 13). *Labrum* robust, with a number of blunt horny tubercles situated aborally. *Mandibles* (fig. 14): a single brush of hairs on inner surface of each mandible, and two bristles on outer surface. *Maxilla:* palp four-segmented; two processes at distal end two-segmented; two blade-like bristles project inwards and a series of bristles extend the length of the maxilla on the inner face, becoming stouter aborally. *Pronotum:* prominent lateral wing-like projections present, extremities beset with bulbous based spines (fig. 16). *Meso- and metanota* larger than pronotum, mesonotum with anterior transverse row of black hairs. *Legs:* prominent spines on ventral edge of prothoracic leg, meso- and metathoracic legs hairy (see figs. 17, 18 and 19 for comparative size). *Abdomen:* white, segments gradually decreasing in size posteriorly, intersegmental grooves shallow; abdominal protuberances present on first segment, dorsal not prominent, lateral disc-like; gills absent; lateral line absent but a series of small " chitinous points " present on segments II to VIII and on segment IX an oblique series of orange-coloured tubercles. *Anal claws* with two unequal auxiliary claws (fig. 20); on dorsal surface anal segment is produced into a pair of lobes, each having two large and several smaller spines. (My specimens each had two large spines but Ulmer states that three may be present.)

Key to the Larvae of the British Beraeidae

Ulmer's (1909) key is modified to include *Ernodes articularis*.

1 Head oval. Gills present in bunches, brush of hairs present on outer aboral edge of mandible. Head bright yellow, heavily marked with black. Clypeus narrow with parallel sides. Black reticulate pattern present on pronotum—in anterior two-thirds many small marks, in posterior third fewer but some larger marks. Tarsal claws of metathoracic legs as long as or longer than tarsal segment. Dorsal anal lobes absent . . . . . **Beraea odesminuta** (L.)

– Head round. Gills absent, brush of hairs on outer aboral edge of mandible absent. Head reddish, generally unicolorous. Clypeus transverse, triangular. Black reticulate pattern on pronotum absent, but wing-like lateral extensions prominent. Tarsal claws of metathoracic legs not as long as tarsal segment. Dorsal anal lobes present 2

2 Ridge on dorsal surface of lateral projection of pronotum straight, well marked and dark in colour. Anal claw furnished with a single auxiliary claw. All bristles on head light in colour **Ernodes articularis** Pictet

– Ridge on dorsal surface of lateral projection of pronotum concave, not well marked, light in colour. Anal claw with two auxiliary claws. Bristles on anterior margin of clypeus black 3

3 Head and pronotum bright brick-red. One brush of hairs only present on inner face of mandibles. Two or three long black bristles arising from each of the two anal lobes dorsal to the anal claws **Beraea maurus** Curtis

– Head and pronotum orange-red. Two brushes of hairs present on inner face of mandibles. A single long black bristle arising from each of the two anal lobes dorsal to the anal claws **Beraea pullata** Curtis

Summary

The larvae of *Beraeodes minuta* (L.), *Beraea maurus* Curtis, *B. pullata* Curtis and *Ernodes articularis* Pictet are described and figured, and a key is given for their separation.

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THE MALE EFFERENT SYSTEM IN *EUBORELLIA ANNULIPES* (LUCAS) WITH SPECIAL REFERENCE TO THE EVOLUTION OF THE GONOPORE IN THE DERMAPTERA

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[Communicated by T. N. Ananthakrishnan]

Introduction

The occurrence of variations in the male efferent system of the Dermaptera, illustrating the stages that may have taken place in the evolution of the gonopore in the Pterygota, has been discussed by Ramamurthi (1958). Reference was also made in the same paper to some interesting features exhibited by *Euborellia annulipes* (Lucas), one of the five individuals on which the study was based. The present paper deals in more detail with the efferent system of this insect.

The cosmopolitan distribution and gregarious nature of *E. annulipes* make it easy to collect nymphs of all stages in good numbers. Only those of considerable size were used, to facilitate dissections, and all stages in the development of the exit tube could be observed. Dissections were carried out in 1 to 2 per cent. saline.

Development of the Genital Tube

The presence of the vasa deferentia right from the first instar nymph, and long before the origin of the exit tube, clearly indicates that these parts of the efferent system are of independent origin and development. The rudiments of the genitalia appear in the penultimate instar nymph and they develop from the inner middle region of the ninth sternum. The rudiment of the exit tube, which makes its appearance early in the last instar nymph, does not project beyond the ninth sternum. At this stage, the common terminal ampulla of the vasa deferentia remains free from the rudiment of the exit tube. Subsequently, an evagination from the ninth sternum puts out a lateral outgrowth and this marks the commencement of growth (fig. 1, *b* and *c*) of the paired region of the future efferent system. By splitting at the centre this lateral outgrowth gives rise to a pair of ducts which are seen to be united at their ends and separate in the middle (fig. 1*d*). The two ends soon establish connections with the common ampulla of the vasa deferentia and the rudiment of the exit tube (fig. 1*e*). Further development of this tube commences only after the course of these events is complete and it elongates considerably before the final moult takes place (fig. 1*f*), when it also becomes traversed by two chitinised grooves which are the future true ejaculatory ducts. During its further development the paired region gives rise to a pair of accessory glands near the base of the seminal vesicle, one on either side. Accessory glands also appear, later, at the junction of the paired and the unpaired regions of

the exit tube. The precursor of the paired region gradually loses its connection with the efferent system and develops into a strongly chitinised hollow structure, projecting into the body cavity. Its continuity with the anterior margin of the ninth sternum is quite distinct and it remains in the adult apparently serving no function.

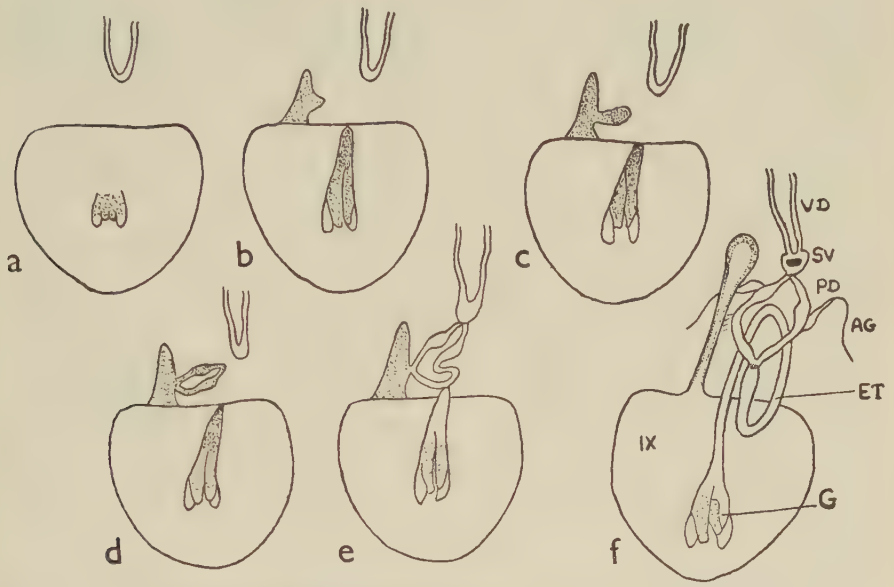

Fig. 1.—Diagrammatic illustration of the development of the genital tube in the post-embryonic stages of *Euborellia annulipes*.

AG, accessory gland ; *ET*, exit tube ; *G*, genitalia ; *PD*, paired ducts ; *SV*, seminal vesicle ; *VD*, vasa deferentia ; *IX*, ninth sternum.

Discussion

The homology of the genital ducts in the pterygote insects has remained a matter for controversial interpretation ever since the time of Wheeler, and it is now agreed that the ejaculatory duct develops as an ectodermal invagination from the ninth sternum, the vasa deferentia and the testes being derived either directly from the segmental coelomic sacs (Seidel, 1924) or from the genital ridge which breaks to form the various gonadal structures (Snodgrass, 1933). Snodgrass (1935) and Pruthi (referred to in detail below) consider the unpaired ejaculatory duct with the single gonopore, in the more recent insect orders, a secondarily derived structure supplanting the primitive paired ducts. The course of development followed by the exit tube (containing both the ejaculatory ducts) in the Dermaptera clearly indicates that the unpaired ejaculatory duct in the Forficulidae is but the persisting member of the original paired ducts, the other undergoing atrophy and loss, or being retained as a vestige at the base of the seminal vesicle, as in *Forficula auricularia* L. This explanation may probably be extended to the other insect orders, loss being one of the most common processes of evolution ; and in the words of Gustafson

(1950) " There has been in the past a tendency to accept the origin and evolution of completely new structures as being rather of common occurrence in the Invertebrates. This tendency was enhanced, of course, by the lack of studies on comparative morphology and the very difficult and ever-present problem of phylogeny within the Invertebrates." He does, however, state that the single penis in *Forficula* may be " the most primitive condition " and the widely separated paired penes in the Labiduroids may represent " the more specialised condition." This view is no doubt based on his belief that the phallic organs are derived from the gonopophyses which, according to him, undergo a fusion in the primitive stage and remain separate from each other in the advanced condition. This belief has also gained support from Nielson (1957), who adds that these organs may have arisen through a fusion of the gonopophyses of segment IX and the limbs of segment X. It is inconceivable that the reduction of the left ejaculatory duct to a vestige in *Forficula* should be considered a primitive condition ; nor does it appear logical to presume that the bipartite condition of the gonoducts in *Anisolabis maritima* (Géné) represents the more specialised condition. Reference may be made here to the suppression of one of the penis lobes in species of *Pseudisolabis*. It is, perhaps, superfluous to refer to such a condition in the Karschiellinae, which is one of the most primitive subfamilies of the Labiduroids. Gustafson's reference to the penis of *Forficula* as being derived by a fusion of the penial rudiments is rather surprising when Qadri (1940) has stated in unmistakable terms that the functional penis in this form is derived from the right penial rudiment, while the rudiment of the left side undergoes suppression during development and is completely lost in the adult, culminating in the left ejaculatory duct being reduced to a vestige.

It is beyond the scope of this paper to enter into a discussion on the homology of the intromittent organ of this group. Nevertheless, the difficulty to be faced in accepting Gustafson's interpretation in view of the nature of the exit tube in the different families, and especially of the development of the exit ducts in *Forficula*, deserves some consideration. Snodgrass (1941) does not discredit the view that " [phallic] lobes are merely outgrowths of the integument at the sides of the gonopore developed specifically to subserve the intromittent function " and states " it is also impossible to see in postembryonic stages of insects any relation of the phallic rudiments to the appendages of the ninth abdominal segment since the latter form the ' coxal plates ' of the definitive ninth sternum." He also draws support from Qadri (*loc. cit.*), who has shown the primary phallic lobes in *Machilis* as developing independently of the ninth segment appendages, and concludes " concerning the origin of the insect phallus we can say only that the facts at present known about the development of the organ . . . appear to favor the view that the phallus is an independent genital structure. The male genital organ of insects has no homolog with a genital function in any other Arthropod group." The disposition of the ejaculatory ducts and the nature of the intromittent organs do not seem to be without bearing on each other in the different families and we may summarise thus their relationship, which has been described in detail in Ramamurthi (1958). The approximation of the ejaculatory ducts in forms like *E. annulipes* seems to represent one stage higher than the comparatively more primitive bipartite condition in *A. maritima*, there being no

change in the paired penes. In the Labiidae, as illustrated by *Marava arachidis* (Yersin), though the penis is unpaired (by fusion or loss?), the ejaculatory ducts are still paired (retaining the condition in *E. annulipes*) but only one of them opens to the outside. In *Forficula*, the intromittent organ on one side is lost and the corresponding duct is reduced to a vestige. There is thus a gradation in the course of development followed by the intromittent organs and the exit ducts (fig. 2) from their paired to unpaired condition in the primitive Labiduroids and the most advanced *Forficula*, respectively. It is also clear that the unpaired condition is established by the reduction or loss of the organs on one

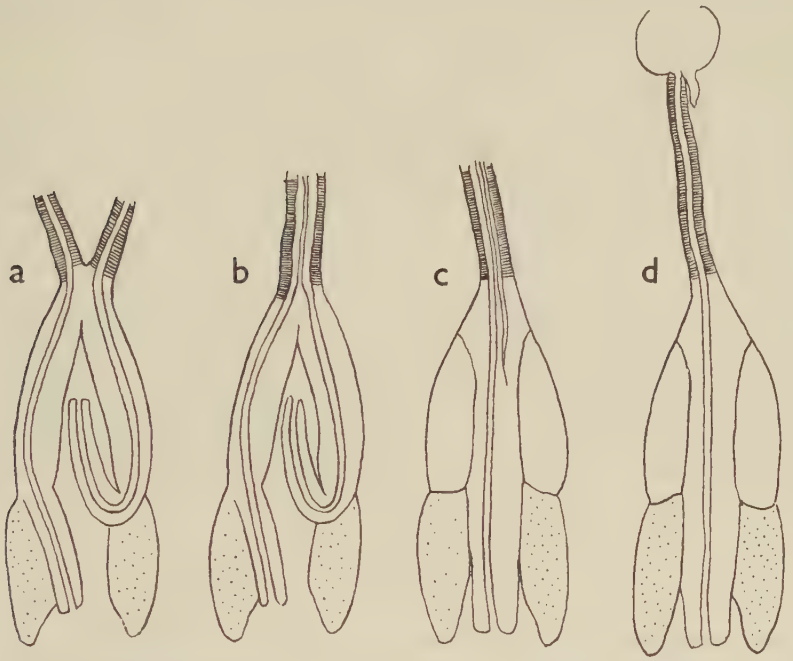

Fig. 2.—Diagrammatic illustration of the stages in the evolution of the gonopore in the different families of Dermaptera.

(*a*) and (*b*) Labiduridae: (*a*) *Anisolabis maritima*, showing the bipartite Ephemeropterous condition; (*b*) *Euborellia annulipes*, showing the approximation of the ejaculatory ducts. (*c*) Labiidae: *Marava arachidis*, with single intromittent organ and paired, but functionally single, ejaculatory duct. (*d*) Forficulidae: *Forficula auricularia*, showing the single functional duct with the other reduced to a vestige.

side and not by the fusion of the paired organs. Hence it seems preferable to consider the phallic organs as arising independently and following the above mentioned course in the different families towards establishing the unpaired gonopore.

The presence of paired and unpaired regions on the exit duct has been observed in orders like the Homoptera, Coleoptera and the Lepidoptera. While the paired region in the latter two has been shown to be nothing more than an anterior bifurcation of the otherwise unpaired ejaculatory duct, its develop-

ment in the Homoptera does not seem to be so simple. Pruthi (1924), basing his study on two Jassids, came to the conclusion that the paired region in the Homoptera was independent of its unpaired counterpart in development, being derived from paired hypodermal invaginations from the eighth sternum. He also believed that these paired ducts, by the mode of their origin, represented the primitive ancestral condition and that the loss of their openings to the outside was consequent on the development, from the ninth sternum, of the unpaired ejaculatory duct, which was thus considered by him (1925) to be the latterly developed secondary structure of the efferent system. Pruthi's view has been severely criticised by George (1932), who did not notice the paired region in *Philaenus*, which is more primitive than the Jassids. George also discusses the difficulty in accepting Pruthi's explanation regarding the relationship of the paired region with the rest of the efferent system.

That it is difficult to compare the paired region of the efferent system in *E. annulipes* with the corresponding structure in the Homoptera is quite obvious. The functional gonopore itself being paired, there is no necessity for another structure to indicate the primitive condition. Further, the paired region, while having an unpaired origin, develops only secondarily from its precursor, which remains free from the efferent system in the adult, serving no other function. It also develops from the ninth sternum itself. In these circumstances a more convincing explanation of the development of the paired region seems to lie in the relationship between it and the accessory glands that may arise in the pterygotes, primarily as a pair of ectodenia. This view may be supported by the fact that accessory glands are not found in other insects of this order so far studied, where the paired region likewise does not occur. This explanation may also be extended to the Jassids, in view of the fact that Pruthi has traced the development of the accessory glands from this region, but in these insects, according to him, the course of development differs.

Summary

1. The development of the genital tube in the postembryonic stages of *Euborellia annulipes* (Lucas) is outlined.

2. The presence of paired and unpaired regions on the exit tube of this insect suggests a parallel with Homoptera and other Endopterygote orders, where a similar condition prevails, but the course of development is quite unique in this species, since here this region arises as a lateral outgrowth of an evagination of the ninth sternum itself, an origin quite different from that shown in the Homoptera.

3. Its ectodermal origin and mode of development seem to suggest that the paired region is specially concerned with the origin of the ectodermal accessory glands.

4. The relationship between the phallic organs and the ejaculatory ducts in the different families of Dermaptera indicates that the unpaired gonopore is derived by a reduction or loss of the primitively paired organs of the exit apparatus, not by their fusion.

5. As in the Homoptera, the paired region develops independently of the main exit apparatus in *E. annulipes*, but the ejaculatory ducts in this insect, unlike those in the Homoptera, are still paired. On the other hand, there is a

gradual reduction of either of the exit ducts in the more advanced members of the Dermaptera, whose exit tube has no paired region. These facts support the following conclusions: (1) the paired region has no homology with the primitive ejaculatory ducts, and (2) the unpaired ejaculatory duct in the more advanced orders of the Pterygota may be the persisting member of the originally paired ducts and not a new structure of the efferent system developed secondarily to supplant the primitive ducts of the mayflies and earwigs.

Acknowledgment

The author expresses his sincere thanks to Prof. T. N. Ananthakrishnan for kindly criticism of the manuscript.

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Postscript

In his recent paper, Snodgrass (1957) further confirms the independent status of the phallic lobes and relates the penis rudiments of the earwigs and mayflies to the primary phallic lobes of the higher insects. The possible objections to this phylogenetic relationship, however, seem to be based on two points, namely (1) the reduction of one of the penial rudiments in the Forficuline earwig that has no parallel in the higher insects, and (2) the penetration of the mesomere by the ejaculatory duct in the Ephemeroptera and Dermaptera, while the unpaired ejaculatory duct in the higher insects does not extend beyond the base of the phallus but communicates to the exterior only by the aedeagal lumen or the endophallus.

* Quoted by Snodgrass (1933).

If we accept the phallic lobes as mere outgrowths of the integument of the ninth sternum, developed specifically for the copulatory purpose, then it may be reasonable to correlate the atrophy of the left penial rudiment in *F. auricularia* with the trend in the evolution of the gonopore. For, considering the tendency of the ejaculatory duct to penetrate the penis in this group, there seems no alternative explanation for the loss of the corresponding exit duct. The suppression of one of the preputial sacs even among members of the most primitive subfamilies in this group could then be interpreted as foreshadowing this evolutionary process ; this is also in contrast to the fusion of the penial rudiments in *Hemimerus*, where the loss of either of the gonopores could not be effected. It may be that consequent on the loss of one of the ejaculatory ducts, the remaining duct, in the higher insects, has lost the tendency to penetrate the aedeagus, and therefore the paired condition of the primary phallic lobes represents only a preservation of the basic structure of the phallic organ. The diversity in the complex pattern of this organ in relation to the fundamental similarity of origin, can perhaps best be understood as a structural adaptation to meet the functional needs of the different orders.

SOME EFFECTS OF LARVAL POPULATION DENSITY ON THE BIOLOGY OF *PIERIS BRASSICAE* L. AND *PLUSIA GAMMA* L.

By M. A. Zaher* and D. B. Long

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Introduction

Population density is generally recognised as being responsible for the production of the forms of locusts known as " phases ", and many investigators have shown differences of a biological nature between these phases. Somewhat parallel effects of population density involving colour and activity were observed in the larvae of Lepidoptera by Faure (1943, 1943*a*). Similar results were obtained by Long (1953, 1955), who also showed certain biological and physiological differences between the larvae of *Plusia gamma* L. bred under solitary and crowded conditions.

Considerable confusion has arisen in the literature as to the precise meaning of the term " phase " as reviewed by Key (1950). Accordingly the use of this term in respect of Lepidoptera has been avoided in this paper, and no attempt has been made to describe the different forms obtained by rearing under solitary and crowded conditions as phases. The earlier work on Lepidoptera had been restricted to the larval stages. An investigation was therefore undertaken of the effect of larval population density on the biology of the adults in two Lepidopterous species. *Plusia gamma* L. and *Pieris brassicae* L.

Technique

The larvae of *P. gamma* and *P. brassicae* were either bred under solitary conditions with one caterpillar per beaker or kept crowded with 50 per beaker, using the method described by Long (1953).

The adult moths of *P. gamma* were kept in one-litre beakers, a newly emerged male and female being set up as a pair in each. On the bottom of each beaker was placed a 9 cm. filter paper on which stood two tubes, 8 mm. × 20 mm., mounted in corks and filled with honey solution and water respectively. In summer the experiment took place in the insectary, while in spring and autumn moths were kept in the laboratory, illuminated by mercury vapour and tungsten lamps for 16 hours per day.

The butterflies of *P. brassicae* from the two larval cultures were kept in separate batches, 30 pairs being put into each cage. The cages were large, 32 in. × 32 in. × 32 in. (fig. 1), as the species needs adequate flying space for mating and depositing eggs. They also need adequate ventilation and sunshine. Accordingly two sides of each cage were made of glass, the bottom of hardboard and the remaining two sides and top of fine terylene net. The terylene net allowed most of the air currents and ultra violet radiations to pass through it.

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Two muslin sleeves were fitted into the net, one on each side, to permit manipulation of materials within the cage. Potted cabbage plants were provided on which the females could oviposit. For feeding, cotton wool which had been soaked in honey solution was placed in a four-inch petri-dish and covered with perforated yellow paper, waterproofed on its under side. In summer breeding took place in the insectary with additional light from mercury vapour and tungsten lamps used for continuous periods of 16 hours per day covering the hours of normal daylight. At emergence the adults were sexed and marked

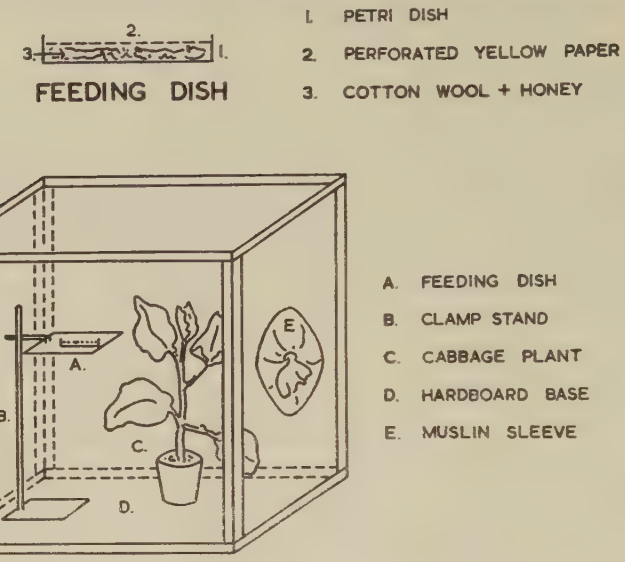

Fig. 1.—The breeding cage for *P. brassicae* (for details see text).

on the wings with a different colour oil paint for each day. The setting up of each experiment, involving 60 pairs of butterflies, covered a period of about four days. Recording thermometers were used for all the experiments.

Five generations of *P. gamma* and four of *P. brassicae* were examined during the two-year course of the investigation. The first generation of *P. brassicae* underwent pupal diapause and was therefore excluded from certain observations. Records were kept of the dates of egg hatching and the individual dates of pupation, adult emergence and death and also the numbers of eggs laid each day.

Egg weights were studied by taking daily eggs laid on the fourth and subsequent days of laying. Eggs were taken in batches of 70 to 80 from adults of both solitary and crowded cultures. Fifty from each batch were weighed wrapped in a cigarette paper of known weight and the remainder of each batch was kept as a control for the estimation of fertility. When this remainder was found to be infertile the whole batch was discarded. In *P. gamma*, where laying takes place mainly during the night, the eggs were weighed in the following morning, but in *P. brassicae*, where egg laying is between 10 a.m. and 4 p.m., they were weighed in the late afternoon. Weighings were continued until a total of 2,500 eggs had been obtained from each treatment, involving two generations of *P. gamma* and one of *P. brassicae*.

Results

Effects on Larval and Pupal Periods and their Interrelationships

P. gamma

The durations of the larval and pupal stages in two generations of *P. gamma* were examined, the first in September 1955 and the second in July 1956, and involved a total of 431 individuals. As previously found (Long, 1953), the duration of the larval period under crowded conditions was less than that in the solitary cultures. The pupal duration, however, was longer in the crowded cultures. These differences in the larval and pupal durations were observed, with one exception, in both sexes and were significant in the case of the females (Table I). The additional duration of the pupal stage in crowded cultures was relatively small so that, as shown in Table I, the total length of their developmental stages was always the shorter of the two. In both conditions of culture the total period was longer for the male than for the female.

Table I.—*The duration in days of the larval and pupal periods in* P. gamma *reared under solitary and crowded conditions*

	Males		Females	
	Solitary	Crowded	Solitary	Crowded
	September 1955			
Larval . . .	29·99	27·21	28·79	26·16
Pupal . . .	18·79	19·50	18·26	19·45
Total . .	48·78	46·71	47·05	45·61
	June/July 1956			
Larval . . .	33·37	30·18	32·64	30·38
Pupal . . .	14·12	14·12	12·68	13·02
Total . .	47·49	44·30	45·32	43·40

A strong negative correlation was obtained in both treatments in both sexes for the relationship between larval and pupal durations, as shown for the generation of September 1955 in figure 2.

P. brassicae

The generation of September 1955, which subsequently diapaused as pupae, and that of July 1956 were examined, 417 individuals being involved. The results were similar to those observed in *P. gamma* in so far as development was generally slower in the male and the larval period was shorter under crowded conditions in both sexes. However, a difference from *P. gamma* was shown in that the pupal period of the non-diapausing generation was also significantly shorter under crowded conditions (Table II), and the total period for these developmental stages was therefore appreciably shorter. In the diapausing generation the pupal period in the solitary cultures was the shorter but the difference was relatively very small when compared with the long pupal period.

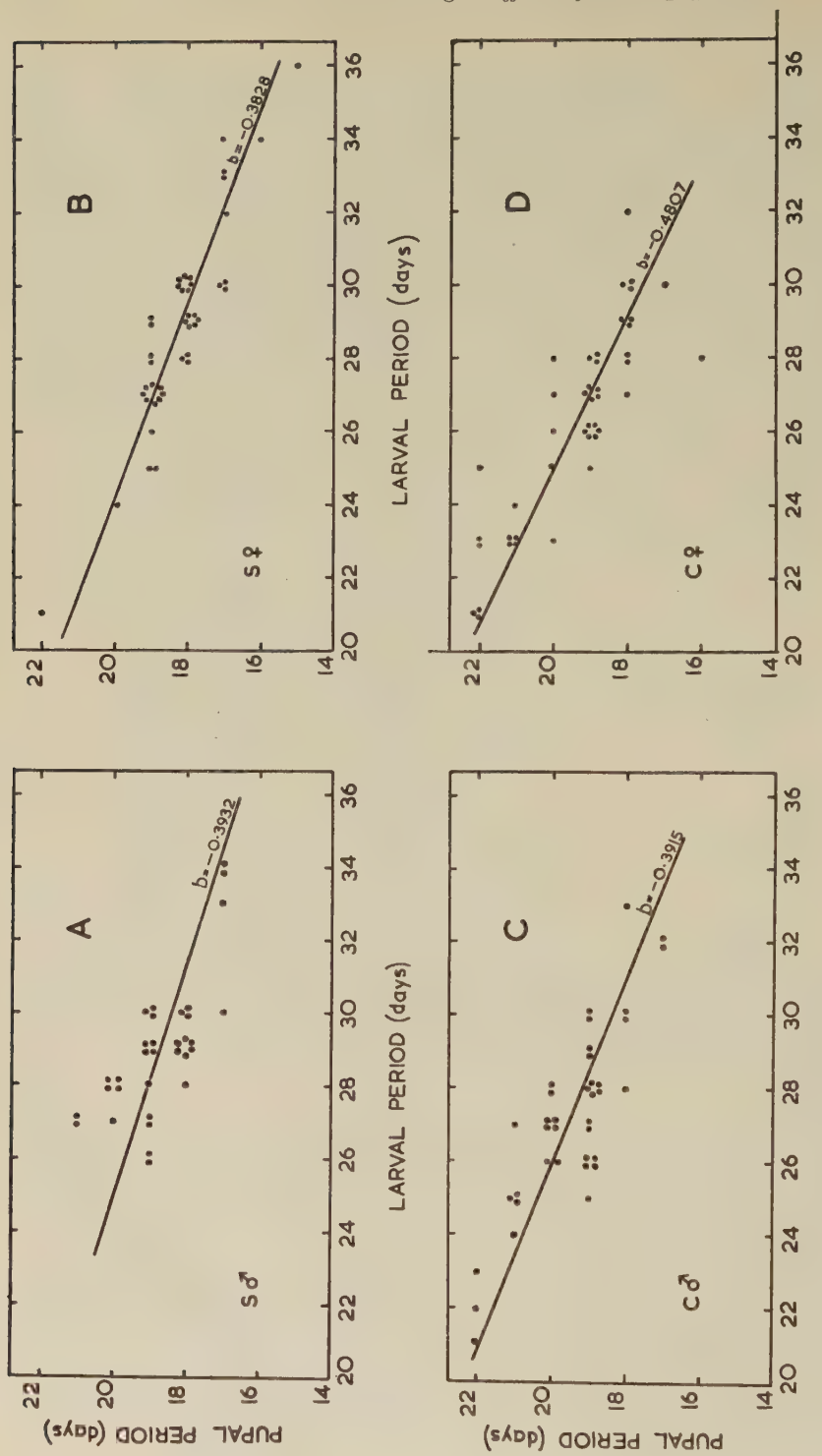

Fig. 2.—The relationship between larval and pupal periods in *P. gamma*: (A) solitary males; (B) solitary females; (C) crowded males; (D) crowded females.

TABLE II.—*Effect of larval crowding on pupal period (in days) in two generations of* P. brassicae, *one of which underwent pupal diapause*

	Males		Females	
	Solitary	Crowded	Solitary	Crowded
Non-diapausing July 1956 . .	14·67	14·15	14·05	13·70
Diapausing September 1955 – .	285·67	287·12	285·39	287·41

Effect of Crowding on the Preoviposition Period

P. gamma

There was a tendency for the preoviposition period in females of *P. gamma* from crowded cultures to be shorter than the corresponding period of females from solitary cultures (Table III), with overall means of 8·6 and 10·2 days respectively, and this difference was significant on two occasions.

TABLE III.—*Preoviposition periods in days in five generations of* P. gamma

	Solitary			Crowded		
Generation	Minimum	Maximum	Mean	Minimum	Maximum	Mean
I	6	13	8·2	5	12	8·2
II	6	16	10·3	5	10	6·8
III	4	17	8·0	3	8	5·5
IV	7	53	18·2	5	44	15·9
V	4	9	6·1	4	9	6·5

P. brassicae

Since 30 pairs of butterflies were kept in each cage, the exact preoviposition period for each female could not be determined but consideration of the available figures showed that the preoviposition period was shorter in the solitary cultures of all three generations.

Effect of Crowding on Fecundity

P. gamma

When comparing the effects of the two larval treatments, both females which did not lay eggs and those which died on the first day of laying were excluded. The results showed a distinct tendency for the females from crowded larval cultures to lay more eggs in four out of the five generations examined, the difference being significant in the first generation (Table IV). The reversal of the effect in the fourth generation may be attributable to a low temperature prevailing throughout this experiment. The females of this generation were rather sluggish and some of them took a very long time, *i.e.* 40 to 50 days, before they began laying and these conditions might favour egg production in the solitary cultures. Nevertheless, when the layings in the crowded cultures for each generation are expressed in terms of those in their solitary counterparts the former laid a mean excess of 15·4 per cent.

TABLE IV.—*The mean numbers of eggs laid per* P. gamma *female in solitary and crowded cultures*

	Solitary					Crowded				
Generation	Pairs used	No. not laying	Pre-mature deaths	Pairs con-sidered	Mean eggs/♀	Pairs used	No. not laying	Pre-mature deaths	Pairs con-sidered	Mean eggs/♀
I	34	5	2	27	218·2	30	4	5	21	352·1
II	11	2	—	9	289·4	10	2	—	8	353·1
III	35	16	3	16	1096·4	32	11	6	15	1263·7
IV	31	6	3	22	822·5	31	8	2	21	594·8
V	12	1	—	11	1342·6	12	1	—	11	1425·9

The frequency distribution of the total numbers of eggs laid is shown in figure 3. As found by Long (1958) for the Wheat Bulb Fly, relatively few

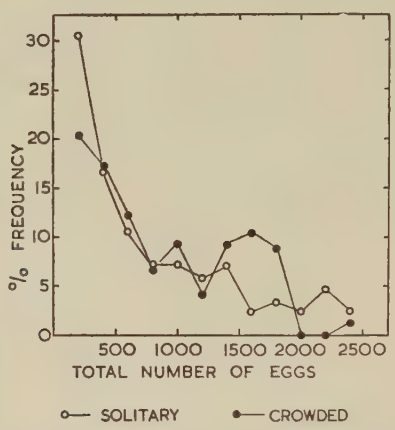

FIG. 3.—The percentage frequency distribution in *P. gamma* of total numbers of eggs laid.

females were responsible for laying most of the eggs. Thus, excluding those which were accidentally killed, in solitary cultures 17 out of 85, or 20·0 per cent., and in crowded cultures 18 out of 76, or 23·7 per cent., laid more than one-half of the total number of eggs obtained from each treatment. From this it can be seen that there was no appreciable difference between solitary and crowded cultures in this respect.

P. brassicae

Observations on four generations of *P. brassicae* indicated that females from solitary cultures had a greater egg-laying capacity than those from crowded conditions. Owing to the necessity of keeping numbers of butterflies together in large cages, difficulties arose in the determination of the number of eggs laid by each female. For this reason three different methods were used for comparing the effect of the treatments. A direct determination of the mean number of eggs laid per female based on the total number of females originally set up in the experiments showed that in three out of four generations

more eggs were laid by the females from the solitary cultures. However, some of these females died before laying began, and the means were therefore calculated for females which lived for a period equal to or longer than the mean preoviposition period (Table V). This estimate could not be obtained for the first generation as records of individual longevity were not kept, but in each of the remaining three generations the total number of eggs laid per female was larger in the solitary cultures. Furthermore there were appreciable variations in the subsequent length of life and these were taken into consideration in determining the mean daily rate of oviposition (Table VI). These results showed that not only were more eggs laid in solitary cultures, but the rate of oviposition was also appreciably greater.

TABLE V.—*Estimates of total numbers of eggs laid per female in solitary and crowded cultures of* P. brassicae

Basis of estimate		Generation I	II	III	IV	Mean
All females used	Solitary	205·5	153·2	117·0	175·7	162·8
	Crowded	39·3	202·1	78·3	61·0	95·2
Females surviving mean preoviposition period	Solitary	.	279·4	223·4	234·2	245·7
	Crowded	.	261·1	163·2	98·3	174·2

TABLE VI.—*Mean numbers of eggs per female laid per day in solitary and crowded cultures of* P. brassicae

	Generation II	III	IV	Mean
Solitary	14·7	15·6	15·6	15·3
Crowded	11·0	9·1	5·0	8·4

Effect in P. brassicae *on the Number of Eggs in a Cluster*

The number of eggs per cluster varied considerably, ranging between 7 and 120. The first generation which underwent pupal diapause produced 83 clusters from the solitary culture and 17 from the crowded treatment. The next two generations together produced 171 and 179 from the solitary and crowded cultures, whilst the last generation produced 82 and 44 clusters respectively from the two treatments. All the experiments showed that a larger number of eggs per cluster was obtained from the solitary treatment (Table VII), but these differences were not significant.

TABLE VII. –*Mean number of eggs per cluster from* P. brassicae *reared under solitary and crowded larval conditions*

	Generation I	II and III	IV	Mean
Solitary	49·9	39·0	50·2	46·4
Crowded	42·8	38·3	31·0	37·4

The Relationship between the Preoviposition Period and Fecundity

As the adults of *P. gamma* were bred as individual pairs it was possible to examine the relationship between the preoviposition period and the total numbers of eggs laid. The results showed in solitary cultures that the shorter the preoviposition period the more eggs were laid and a negative regression was obtained (fig. 4, A). Similar negative regressions were also obtained with

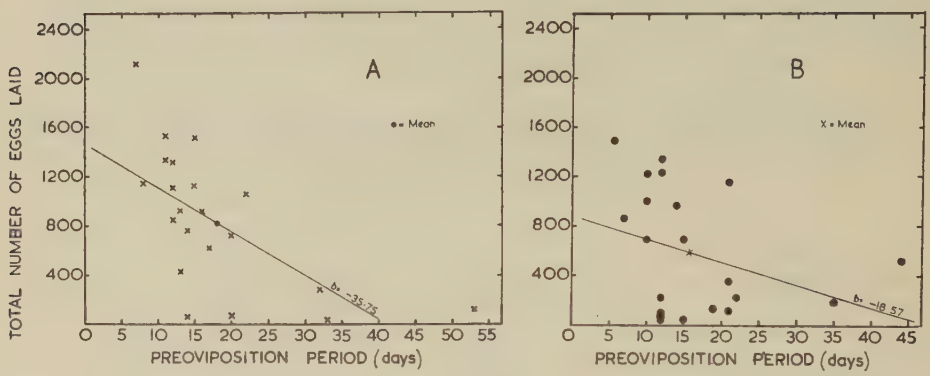

FIG. 4.—The relationship between the preoviposition period and the total number of eggs laid: (A) from solitary culture; (B) from crowded culture.

crowded cultures (fig. 4, B), the differences being apparent in the position of the mean points due to the effect of crowding. It was not possible to determine from the data whether crowding actually produced a displacement of the regression line, or by reducing the preoviposition period tended to involve more of one extreme of the naturally occurring variation. However, the latter would appear to be the more probable since comparable levels in fecundity were observed for a given preoviposition period in both solitary and crowded cultures.

No correlations were obtained between the length of the laying period and the total number of eggs laid.

Effect of Crowding on the Weight of the Egg

P. gamma

Out of 2,500 eggs which were taken in groups of 50 from each condition of culture in *P. gamma* and weighed, 2,350 from solitary and 2,150 from crowded cultures proved fertile and were contrasted. The results showed that the mean weight per group was greater in solitary cultures, the difference being significant in both generations (Table VIII). The slightly larger differences existing between the generations could be attributed to the season. At higher prevailing temperatures the August generation developed more rapidly, producing a smaller adult (Long and Zaher, 1958) and laying a smaller egg. Thus in these respects the effects of crowding resembled those of temperature.

TABLE VIII.—*Mean weight in mg. of groups of* 50 *eggs from two generations of* P. gamma *reared under solitary and crowded conditions*

Generation		No. of observations	Weight of 50 eggs		Difference between means with S.E. (solitary–crowded)
			Mean	S.D.	
June	Solitary	20	4·93	0·44	+0·31±0·13
	Crowded	22	4·62	0·42	
August	Solitary	27	4·46	0·51	+0·51±0·12
	Crowded	21	3·95	0·34	

S.D. = Standard deviation. S.E. = Standard error.

P. brassicae

Similar significant results were obtained in *P. brassicae* from weighings of 2,550 eggs from both treatments, the egg weight being greater in solitary cultures (Table IX). As in *P. gamma*, larval crowding had been found to produce a smaller adult (Long and Zaher, 1958).

TABLE IX.—*Mean weight in mg. of groups of* 50 *eggs from* P. brassicae *reared under solitary and crowded conditions*

	No. of observations	Weight of 50 eggs		Difference between means with S.E. (solitary–crowded)
		Mean	S.D.	
Solitary	51	10·47	0·62	+0·60±0·11
Crowded	51	9·87	0·50	

S.D. = Standard deviation. S.E. = Standard error.

The Effect of Crowding on Longevity and its Relationship with Fecundity

P. gamma

The longevity in both sexes was found to vary considerably between individuals from the same larval treatment. A few adults died within the first four days after emergence and were excluded from the observations as most of them did not take any food. The results given in Table X show that the

TABLE X.—*Mean adult longevity in days in* P. gamma *from solitary and crowded cultures*

Generation	Males			Females		
	Solitary	Crowded	Crowded as % solitary	Solitary	Crowded	Crowded as % solitary
I	14·3	16·5	115·38	21·2	22·7	107·08
II	25·1	25·8	102·79	30·5	27·6	90·49
III	35·4	29·8	84·18	30·8	28·8	93·51
IV	29·3	35·7	121·84	36·0	39·9	110·83
V	22·4	25·8	115·18	20·8	23·4	112·52
		Mean	107·87		Mean	102·88

females from crowded cultures lived longer than did those kept under solitary conditions in three out of five generations, whilst the males lived longer in four out of five. When the longevities of the crowded cultures were expressed as a percentage of the solitary ones, the males more clearly showed a slight tendency to live longer in crowded cultures.

In solitary cultures 15 out of 101, or 14·9 per cent., of the females failed to lay at all, whilst in crowded cultures 19 out of 96, or 19·8 per cent., failed. This compares favourably with the 27 per cent. failure observed in females of the Wheat Bulb Fly (Long, 1958). The difference between the percentage failures in the two conditions of culture was not significant and it would appear unlikely that larval crowding influenced the subsequent sterility, as a larger number of sterile females appeared in only two out of the five generations

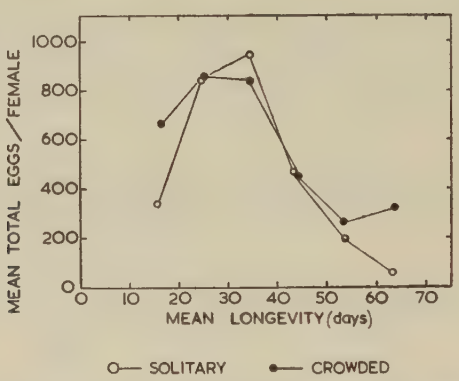

Fig. 5.—Mean longevity (grouped in 10-day intervals) and the mean number of eggs laid per female.

under crowded conditions. Furthermore, crowding did not appear to influence the longevity of sterile females for, whereas some females which did not lay eggs died within two or three days, others lived virtually as long as their egg-laying sisters. Thus in both solitary and crowded cultures we found sterile females living up to 62 days, whereas fertile females lived up to a maximum of 64 days.

The results showed that it was not the females which lived longest which layed the largest numbers of eggs, but those which lived roughly one half of the maximum period (fig. 5). Earlier dying females laid more in crowded than in solitary cultures. The relatively high mean value obtained for the total number of eggs in the longest lived females in the crowded culture of figure 5 was probably due to the fact that only two females contributed to this mean, one of which laid a large number of eggs.

P. brassicae

During the course of the experiments it was found that a large percentage of adults, especially males, died within four days of emergence. David and Gardiner (1952) stated that the majority of their laboratory bred butterflies only lived from five to thirteen days. These early deaths were probably due

to the artificial conditions of breeding, and the problem therefore needs further study. However the results given in Table XI show that the females from crowded cultures lived longer than their solitary counterparts, whilst there was no difference between the males from the two larval treatments. The females in both cultures lived longer than their respective males.

TABLE XI.—*The longevity in days of adults of* P. brassicae *from solitary and crowded larval cultures*

Generation	Males		Females	
	Solitary	Crowded	Solitary	Crowded
II . . .	9·0	9·5	15·5	23·3
III . . .	8·9	8·0	12·5	15·8
IV . . .	14·2	14·5	18·0	19·4
Means . . .	10·7	10·7	15·3	19·5

DISCUSSION

The results of these experiments have shown that the conditions of larval culture may affect a number of factors throughout the remainder of the animal's life. The results have also shown that the direction of the change produced may differ according to the species. Principal amongst these effects was that on the rate of development. As earlier shown by Long (1953), in *P. gamma* and in *P. brassicae* crowding decreased the larval duration. Since a negative relationship has been found to exist in *P. gamma* between this and pupal duration, crowding naturally led to a more prolonged pupal period in this species. Whether this longer period was at all due to the reduction in the number of instars associated with crowded conditions (Long, 1953) remains to be determined. In *P. brassicae*, however, larval crowding reduced both the larval and the pupal periods.

The overall effect of larval crowding on the developmental stages from hatching to subsequent egg laying was the same in both species in that the time involved was less in crowded cultures. Chauvin (1941) found that the developmental stages of the locust *Schistocerca gregaria* L. were reduced by crowding, and Utida (1941) obtained similar results with the bean weevil *Callosobruchus chinensis* L. Some of the factors responsible for this effect of crowding in Lepidoptera have been considered by Long (1953, 1955) and Long and Zaher (1958).

It seems possible that some connection exists between the relative lengths of the pupal and preoviposition periods. It was found in crowded cultures that, whereas in *P. gamma* a shorter preoviposition period followed a longer pupal duration, in *P. brassicae* the shorter pupal period was followed by a longer preoviposition period. The pupal stage is important for the laying down of adult characters and has been termed an adult instar by Hinton (1948). It would appear reasonable to believe, therefore, that the longer pupal periods of crowded *P. gamma* and solitary *P. brassicae* may influence the degree of egg differentiation, for it was shown in *P. gamma* within each condition of culture that the largest numbers of eggs were laid by females having a short preoviposition period, whilst in both species the larger number of eggs were laid in the

condition of culture producing the longer pupal period. However, the length of the pupal period cannot be the sole factor in *P. gamma* in determining the number of eggs subsequently laid, for Zaher (1957) showed that when adults from the same conditions of larval culture were slightly crowded, the preoviposition period was shortened and this also was followed by an increased fecundity.

It is interesting to note that the naturally occurring negative relationship existing in *P. gamma* between the preoviposition period and the total number of eggs subsequently laid, as found in solitary cultures, was not due to the length of the laying period. Crowding, in shortening the preoviposition period and producing more eggs, appears to accentuate one extreme of this relationship, presumably owing to the earlier effects on the larval and pupal durations rather than to the initiation of an entirely new response.

Larchenko (1936) showed in the moth *Loxostege sticticalis* L. that there was a direct relationship between the fat content of the larvae and the number of eggs deposited. One of the effects of crowding in the larval stage of *P. gamma* is a relatively larger fat content prior to pupation (Long, 1953). The pupae and adults of crowded cultures, however, contain less fat than their solitary counterparts (Long and Zaher, 1959). From this it follows that there was a greater utilisation of fat in the prepupal stage under crowded conditions, and it was possible that this was involved in the development of the gonads and the larger number of eggs produced.

The differences between the effect of crowding on *P. gamma* and *P. brassicae* appear to be related to the degree of deviation from the normal experience of the species. In *P. gamma* the eggs are loosely scattered and the larval experience tends towards that of the solitary individual. In *P. brassicae*, however, the eggs are laid in tightly packed clusters and larvae habitually spend the early part of their lives in dense aggregations (Long, 1955). Thus in *P. gamma* experimental crowding, which showed the consistent effect of shortening the larval duration, led to a prolonged pupal period, a short preoviposition period and the laying of the larger number of eggs. In *P. brassicae*, however, the more abnormal condition of isolation prolonged the larval and pupal periods but led to a shorter preoviposition period and the laying of a larger number of eggs. It is tentatively suggested that these are a dependent series of effects and that they constitute, in terms of species survival, a compensatory response to abnormal population densities on the part of the developing individual in producing larger numbers of offspring.

Summary

A study of some of the biological effects of larval population density in Lepidoptera has shown that in *P. gamma*, although crowding prolonged the pupal period, it shortened the larval and preoviposition periods so much that the total developmental period from hatching to egg laying was shorter than under solitary conditions. In both larval treatments a long larval period was followed by a relatively short pupal period, and a short preoviposition period by the laying of large numbers of eggs. The subsequent fecundity was greater in crowded cultures, though under both conditions of culture more than one-half of the eggs were laid by slightly more than 20 per cent. of the females.

In *P. brassicae* the shorter larval period in crowded cultures was followed by a shorter pupal but a longer preoviposition period, and the total developmental period was, as in *P. gamma*, shorter than under solitary conditions. The subsequent fecundity was, however, less, with fewer eggs per cluster.

In both species the mean egg weight was lighter in crowded cultures.

There was a tendency for the adult longevity of the male in *P. gamma* and of the female in *P. brassicae* to be longer under the crowded treatment. Larval crowding in *P. gamma* did not influence either the percentage of sterile females or their longevity.

Acknowledgments

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ON THE DISTRIBUTION AND SEASONAL INCIDENCE OF CULICINE MOSQUITOES IN SOUTHERN NIGERIA

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Introduction

In 1956–57 research on yellow fever in Southern Nigeria included an ecological study on the main urban vector of the virus, *Aëdes* (*Stegomyia*) *aegypti* L. During this study data were also gathered on the breeding habits and seasonal incidence of several other culicine species found in the area. The site of these investigations was the village of Ilobi (6° 45′ N., 3° 5′ E.), some 50 miles north-west of Lagos by road, situated in climax rain forest and isolated from surrounding rural areas.

The south-west region of Nigeria can be divided into three vegetational zones—a coastal strip of mangrove swamp, a narrow belt of freshwater swamp extending up to 10 miles inland and a more extensive area of rain forest, which is found up to 200 miles inland. The climate of the area is such that the year can be divided into two distinct seasons. The dry season extends from November to February or March and is characterised by very little rain and temperatures up to 105° F. The wet season commences with scattered showers and storms in March, the wettest months being May to July, during which some 30 inches of rain fall. Throughout the rainy season the maximum temperature rarely rises above 85° F. August is dryer and sometimes warmer with the last rains coming in September and October. The yearly rainfall is between 60 and 80 inches and the maximum relative humidity is always 100 per cent., the minimum varying between 60 per cent. for the dry season and 85 per cent. for the wet. On the coast the average wind speed is about 7 miles per hour.

The village, which is about half a mile across, is surrounded by several distinct vegetational zones. To the north is an area of farmland, the main crops being cassava (*Manihot* sp.), yam (*Dioscorea* sp.), cocoa yam (*Xanthosoma sagittifolium*) and some fruit, including pineapple (*Ananas comosus*) and banana (*Musa sapientum*). To the east there is scrub which represents an early stage in forest recolonisation of farmland, running into true forest about 100 yards beyond the village. To the south is early forest, characterised by a broken canopy, dense shrub growth and patches of farmland and cocoa. The western side of the area is taken up by an extensive cocoa plantation in which there are scattered patches of pineapple.

The study described here falls into three divisions, a survey of natural larval habitats, an investigation into the distribution and succession of the species with respect to the different vegetational zones and observations on the seasonal incidence of the major species. Examples of studies of this nature are lacking for this area, although there are a number of scattered references

to the larval habitats of the commoner species. As a result of these studies it was evident that in this particular area each of the major species bred in a restricted zone, within which they showed marked breeding site preferences and that the seasonal fluctuations in numbers were not directly correlated with rainfall.

Survey of Larval Habitats

This part of the study was carried out to establish the typical larval habitats of the culicine species occurring in the area. These habitats have been divided into domestic containers, tree-holes, leaf axils and floor containers, the occurrence of the species in each of these being shown in Table I.

Table I.—*The number of occurrences of culicine larvae in natural habitats in the region of Ilobi Village in South-western Nigeria*

Habitat	Domestic containers	Tree-holes	Snail shells	Cocoa husks	Gourd shells	*Xanthosoma* axils	Banana axils	Pineapple axils	Rolled leaves
Total sampled	237	25	252	730	31	297	88	280	50
A. aegypti	49	.	2	.	.	.	1	.	.
A. apicoargenteus	1	5	.	.	8	.	1	1	.
A. simpsoni	.	.	.	.	.	.	1	.	.
A. longipalpis	1	5	.	.	.	.	.	.	.
A. luteocephalus	.	1	.	.	.	.	.	.	.
C. albiventris	1	1	.	.	.	.	.	.	.
C. nebulosus	1	.	.	6	.	.	.	.	.
C. cinereus	1	.	.	.	1	.	.	.	.
C. duttoni	10	1	.	.	.	.	.	.	.
C. tigripes	1	.	.	.	.	.	.	.	.
C. horridus	1	.	.	.	.	.	.	.	.
M. brevipalpis	3	.	.	.	.	.	1	1	.
E. chrysogaster	.	.	7	177	10	1	3	1	4
E. oedipodius	1	.	2	.	.	1	2	1	4
E. pencillatus	.	.	15	.	.	.	.	.	.
E. sylvestris	.	.	.	.	.	.	.	.	4
E. quinquevittatus	.	.	9	.	.	.	.	.	.
H. taeniarostris	.	.	.	.	.	5	.	20	.

Domestic Containers

The domestic containers consisted of clay pots used by the local population for water storage, the capacity varying between 0·5 and 8 gallons. The water in them was generally free from contamination and at a lower temperature than the surrounding atmosphere owing to the continual evaporation from their porous surfaces. The commonest species in this type of habitat was *A. aegypti*, and *Culex* (*Culex*) *duttoni* Theobald was less common. *A. aegypti* had a well defined pattern of breeding behaviour, 55 per cent. of the larvae being found in pots inside houses, 30 per cent. outside houses but in otherwise sheltered positions and 15 per cent. in fully exposed pots. *C. duttoni* was confined to exposed pots. In passing it may be noted that *Anopheles* (*Myzomyia*)

gambiae Giles was more common in exposed pots than elsewhere in the village. Predators were rare in these containers, *Culex* (*Lutzia*) *tigripes* Grandpré and Charmoy and *Megarhinus brevipalpis* Theobald being recorded only on very few occasions. Several other species were taken but only rarely and in small numbers, these being *Aëdes* (*Stegomyia*) *apicoargenteus* Theobald, *A.* (*Finlaya*) *longipalpis* Grunberg, *Culex* (*Culiciomyia*) *cinereus* Theobald, *C.* (*Culiciomyia*) *nebulosus* Theobald, *C.* (*Neoculex*) *albiventris* Edwards, *C.* (*Neoculex*) *horridus* Edwards and *Eretmapodites oedipodius* Graham. *C. cinereus* was taken from a clay pot in which the water was heavily polluted with animal excrement. Association of species was rare, *A. longipalpis* and *M. brevipalpis* being recorded together once, as also were *A. aegypti* and *C. duttoni*. A few large iron drums were found in the village which were also used for water storage, but the only species taken from them was *C. duttoni*.

Tree-holes

The majority of the tree-holes in the area were found in the cocoa plantation, although they seldom contained larvae. A few were also located in the late forest to the east of the village. The water in these habitats was nearly always contaminated with large amounts of decaying vegetable debris. When sampling, the water and debris were emptied on to a white enamel tray which was then filled with water and in this way any larvae could be located. The commonest tree-hole species were *A. longipalpis* and *A. apicoargenteus*, these being found in the forest to the east, whilst *A.* (*Stegomyia*) *luteocephalus* Newstead, *C. duttoni* and *C. albiventris* were taken from tree-holes in the cocoa plantation. No predators were found in any of these habitats. They did not retain water over the dry season and dried debris taken from them did not yield any larvae on soaking.

Leaf Axils

The leaf axils of bananas, pineapples and cocoa yams all provided larval habitats. The water varied in purity according to the position of the axil on the plant. In bananas the purest occurred in the highest axils, this presumably being the freshest, whilst in both the pineapple and the cocoa yam the purest water was found in the outermost axils. In these latter two species the exposed outer axils collected more plant debris than the enclosed ones. Another important feature of the leaf axils was that they retained water for long periods, in some cases over the dry season, which made them more permanent habitats than the others now discussed. The commonest leaf axil breeder was *Harpagomyia taeniarostris* Theobald, which was largely restricted to pineapple axils in the cocoa plantation. On a few occasions it was taken from cocoa yam axils to the south of the village and at all times the larvae were found in clear uncontaminated water. The only other species found in cocoa yam axils were *Eretmapodites oedipodius* and *E. chrysogaster* Graham. Several other species were recorded from leaf axils, but none in great abundance. *E. chrysogaster* was taken from banana axils in the forest on the east on more occasions than any other larvae. *A.* (*Stegomyia*) *simpsoni* Theobald, *A. apicoargenteus*, *A. aegypti*, *M. brevipalpis* and *E. oedipodius* were also taken from these axils. These species were found in the more contaminated water.

Pineapple axils yielded, on single occasions only, *A. apicoargenteus*, *M. brevipalpis*, *E. oedipodius* and *E. chrysogaster* as well as *H. taeniarostris*. Generally the leaf axils did not provide an abundant larval fauna. *Forcipomyia* spp. were widespread, these and *Chironomus* spp. being taken from the more contaminated water.

Floor Containers

These included cocoa husks, gourd shells and snail shells, all of which contained large amounts of vegetable debris, and rolled leaves. The snail shells (*Achatina isabella*) were widely distributed, having been left lying on the ground after the death of the snail, and usually contained from 50 to 300 cubic centimetres of water which was dark brown in colour. The commonest species in these shells were *Eretmapodites quinquevittatus* Theobald and *E. pencillatus* Edwards, whilst *E. oedipodius* and *E. chrysogaster* were less abundant. *A. aegypti* was found breeding in snail shells on the village edge on two occasions. The decaying cocoa husks were very abundant on the floor of the plantation and during the rainy season would hold water for long periods before finally decomposing. The water in these containers was always dark brown and rich in decaying plant tissues. These husks mostly contained large numbers of *E. chrysogaster* and on a few occasions *C. nebulosus*. Throughout this survey no other species were found breeding in these containers. Decaying gourd shells were not common. Of the 31 sampled, only 19 were found to contain mosquito larvae, the commonest species being *E. chrysogaster* and *A. apicoargenteus*, whilst *C. cinereus* was taken only once. Rolled leaves typically contained clean water and did not support an extensive larval fauna, *Eretmapodites sylvestris* Ingram and de Meillon and *E. chrysogaster* being recorded on a few occasions with *E. oedipodius*.

Distribution and Succession

From the preliminary survey of larval habitats it was apparent that most species were restricted in their breeding to a particular area. It was therefore decided to study this distribution in more detail and to ascertain if a succession of species existed. The eastern side of the area was chosen because it showed a transition from village to forest conditions. The investigation was carried out by setting up a transect of experimental breeding sites extending from the centre of the village to 600 yards inside the forest. Along this transect were placed eleven sampling stations, each consisting of a clay and a bamboo pot; these two types of container simulated both the typical urban and forest larval conditions. The clay pots were about 15 inches in diameter and 12 inches deep, whilst the bamboo pots were 4 inches across and 15 inches deep. These held about 4 pints and 1 pint of water respectively. The pots were sampled weekly throughout the year 1956 and the larvae present were noted; this indicated the extent of breeding of each species. The results are summarised in Table II and show the number of times throughout the year that each species was recorded at each station.

A. aegypti was largely restricted to the village, where breeding was continuous throughout the year. There was some evidence of breeding in the scrub-zone, but this was restricted to the hotter and dryer months as the species

was not found beyond the village in the rainy season. It may be suggested that breeding beyond the normal range was due to extreme climatic conditions prevailing in the village at these times. Breeding was more common in clay than in bamboo pots.

Larvae of *A. apicoargenteus* were found at all points of the experimental transect, breeding being continuous in the scrub-zone, where it was the most abundant species. They were less common in the forest and least common in the village. *C. nebulosus*, *C. albiventris* and *M. brevipalpis* also were found breeding in the experimental pots in the scrub-zone, and *A. longipalpis*, *A. luteocephalus*, *C. cinereus* and *E. chrysogaster* on a few occasions.

TABLE II.—*The number of occurrences throughout the year of culicine larvae in the sampling stations along the east transect*

	Village			Scrub			Forest				
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
A. aegypti	64	58	66	17	5	4	2	3	1	1	.
A. apicoargenteus	8	8	7	31	34	35	28	13	15	6	7
A. longipalpis	.	.	.	2	2	1	3	4	6	1	2
A. luteocephalus	1	.	.	.	.	1	2	2	1	.	.
A. simulans	.	.	.	.	.	.	.	.	.	4	3
C. nebulosus	5	3	.	9	17	12	21	12	11	19	6
C. cinereus	.	.	.	.	.	2	.	.	.	.	.
C. albiventris	.	1	.	14	1	14	15	37	32	25	21
C. tigripes	.	1	.	4	.	.	.	.	.	.	.
M. brevipalpis	.	1	.	8	10	7	5	14	11	4	4
E. chrysogaster	.	.	.	.	6	7	7	5	5	10	.
E. oedipodius	.	.	.	.	.	.	2	.	.	.	4

E. chrysogaster and *C. albiventris* were abundant in the forest and were the commonest species found breeding in this zone. Although the latter species was found to extend its breeding areas to the forest margin only in the wet season, spasmodic records show that *E. chrysogaster* did so at all seasons. Also breeding in the forest were *A. apicoargenteus*, *A. longipalpis* and *A.* (*Aëdimorphus*) *simulans* Newstead and Carter. It is interesting to note that the two predators, *E. chrysogaster* and *M. brevipalpis*, were never found breeding in the same pot at the same time and the presence of the latter species was usually associated with the absence of *C. nebulosus*. A series of bamboo pots were placed at intervals up a tree 330 yards inside the forest and sampled weekly for mosquito larvae. Over the year it was found that *C. albiventris* bred more commonly at ground level, *C. nebulosus* at 25 feet and *A. apicoargenteus* at 50 feet. *E. chrysogaster* was taken at all points an almost equal number of times.

Although some of these species were taken at all points along the transect, a pattern of succession became evident which, running from the village to the forest, may be summarised as follows : *A. aegypti*, *A. apicoargenteus*, *C. nebulosus*, *M. brevipalpis*, *E. chrysogaster*, *C. albiventris*, *A. longipalpis* and *A. simulans*.

Seasonal Incidence

To study the seasonal incidence of the species breeding within this area, sampling stations were set up in each of the vegetational zones around the village. Each station consisted of a clay and bamboo pot as described in the previous section, and in each area there were the following number of stations, village (2), scrub-zone (1), forest (2), cocoa plantation (4), and early forest to the south (3). Each of these stations was sampled weekly and the number of larvae of each species recorded. Table III gives an indication of the relative abundance by presenting the results as the total number of larvae found each month over the whole area. Only five species are discussed here, as the others were present in numbers too small to allow any conclusions to be drawn. The fluctuations of the species, with the exception of *E. chrysogaster*, followed a general pattern throughout the year, and showed an increase in numbers at

Table III.—*The monthly totals of culicine larvae over the whole area studied*

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
A. aegypti .	203	1,235	1,355	1,318	604	654	441	1,162	421	544	280	607	8,824
A. apicoargenteus	448	413	399	849	499	.	116	236	630	500	519	212	4,821
C. albiventris .	380	392	860	929	656	420	149	285	98	245	198	279	4,891
C. nebulosus .	68	872	189	554	444	.	140	40	217	248	57	186	3,015
E. chrysogaster	129	88	7	14	94	.	39	387	101	236	548	19	1,662
Total .	1,228	3,000	2,810	3,664	2,297	1,074	885	2,110	1,467	1,773	1,602	1,303	23,213

the beginning of the rains with a peak about April, then a decline in the mid-rainy season, followed by a further peak in August to September before the final decline at the end of the year. This mid-year drop in numbers has also been indicated for the adults in biting studies carried out in the area over the same period (Boorman, 1956). This was particularly plain with *A. aegypti*, where the decline in adult numbers came about one month after the decline in larval numbers, the same lag being observed with the August to September increase.

The breeding intensity of *A. aegypti*, as would be expected from the previous study, was greatest in the village ; the only other area with any considerable breeding was in the cocoa plantation. The monthly fluctuations followed the general pattern outlined above. The clay pots provided 83 per cent. of the larvae whilst the numbers in the bamboo pots in any area were small and irregular. In the scrub-zone and early forest the peak at the beginning of the year came two months before that in the village, and the one in the cocoa one month before. The numbers in these areas declined throughout the rest of the year, but there was a further increase in the cocoa plantation one to two months after the final peak in the village. This may suggest that the breeding population at the beginning and end of the hot season found less extreme conditions in these areas and that the population build-up took place here and subsequently in the village. *A. apicoargenteus* bred with greatest intensity in the scrub-zone, with decreasing intensity in the forest, cocoa plantation, early forest and village. In each of these areas there were two population maxima, which in the case of this species may be correlated with leaf-fall.

There is a major leaf-fall at the end of the dry season and a minor one toward the end of the wet season and, as this species was found to breed in water contaminated with decaying vegetable matter, this factor may well influence the seasonal abundance. The greatest breeding intensity of *C. nebulosus* was in the scrub-zone, but here and elsewhere the numbers fluctuated without any apparent correlation with observable environmental factors. About 80 per cent. of the breeding was in bamboo pots. The breeding of *C. albiventris* was confined largely to the early forest with lesser intensity in the forest to the east. It was not found elsewhere. There was an increase in numbers in the early part of the year but a steady decline throughout the succeeding months. *E. chrysogaster*, which bred with comparable intensity in both of these zones, fluctuated irregularly throughout the year. The large numbers in the later months of the year may have been due to the accumulation of cocoa husks at the end of the rainy season, which provided a greater number of potential breeding sites.

The following observations may be made with regard to inter-specific competition. *E. chrysogaster* bred in the early forest and cocoa plantation but *M. brevipalpis* was absent from these two areas. Furthermore, *M. brevipalpis* bred with some intensity in the scrub-zone where *E. chrysogaster* was less common. It is of further interest that the percentage of *A. apicoargenteus* breeding in clay pots along the eastern transect varied, being 13 per cent. in the village, 31 per cent. in the scrub-zone and 63 per cent. in the forest. This may be the result of a dual competition, for in the village 83 per cent. of the breeding of *A. aegypti* was in the clay pots, whilst in the forest 80 per cent. of the *C. albiventris* breeding was in bamboo pots.

Discussion

Shannon (1931), as a result of mosquito studies in South America, stated that the larvae of each species are more or less restricted to a special type of habitat ; and further, that the natural classification of the habitats is in accord with the natural classification of the family as based on larval and adult characters. Considering the first part of this statement in the light of the present study, and of the observations of other workers, we must conclude that, though this may be true for some species in some parts of their range, it is not always true throughout their range, and that other species have a more plastic breeding behaviour. Thus *A. aegypti*, which in this area was found to be restricted to domestic containers, had previously been taken from tree-holes and crab holes in Nigeria (Dunn, 1928 ; Riqueau, 1929), whilst the writer had found it breeding elsewhere in a rock pool (Surtees, 1958*a*) In East Africa, Haddow *et al.* (1951) found this species breeding in forest areas in tree-holes. *A. apicoargenteus* has also been found in a wide variety of larval habitats ; Hopkins (1952) observed that it was common in tree-holes, whilst Harris (1942) found it also breeding in rock pools and water pots. A similar species is *C. nebulosus*, which has been recorded in West Africa from *Colocasia* axils, domestic containers, tree-holes and flower heads (Bacot, 1916 ; Dalziel, 1920 ; Kerr, 1933 ; Surtees, 1958*a*). In East Africa it was found to be very common in tree-holes (Haddow *et al.*, 1951). Another plastic species is *M. brevipalpis*, which was recorded in the present study from domestic containers and leaf axils and had previously been found in tree-holes and bamboo cuttings in West Africa

(Hopkins, 1936; Philip, 1933). Haddow and others have taken it from tree-holes and domestic containers in East Africa.

Larval studies on the other species found in the Ilobi area indicate that they have more rigid breeding patterns. *A. simpsoni*, which in the present study was found only in banana axils, also appears to have a restricted breeding behaviour elsewhere; the writer found the species breeding abundantly in banana and pineapple axils in Ghana. Gibbins (1942) found it a typical axil breeder in East Africa. Similarly, *H. taeniarostris* was found exclusively in leaf axils in Nigeria and Ghana by the writer, and in the same type of habitat throughout West and East Africa by Hopkins (1936) and Haddow (1948). The *Eretmapodites* larvae appear to have restricted larval habitats. Kerr (1933) pointed out that *E. chrysogaster* was common in all cocoa growing areas throughout West Africa, and at Ilobi the larvae of this species were most abundant in the decaying husks in the cocoa plantation. Bequaert (1930) and Mattingly (1952) made similar observations during their studies in this area. During the present study *E. quinquevittatus* was only taken from snail shells, and Lumsden (1955) found it in the same habitat in East Africa. *E. pencillatus*, both here and in East Africa (Haddow, 1946), has been taken only from snail shells. *E. oedipodius* is an exception in this genus, having been reported in leaf pools in both West and East Africa (Hopkins, 1936; Haddow, 1946), and at Ilobi in snail shells, leaf axils, rolled leaves and domestic containers.

With regard to the second part of Shannon's statement, it should be pointed out that ecological studies on several groups of animals, including insects, indicate that closely related species occupying the same geographical locations tend to have different habits and habitats. This has been demonstrated for birds (Longstaff, 1926; Lack, 1945), mammals (Dice, 1931), crabs (Crane, 1941) and anopheline mosquitoes (Ribbands, 1944). Mayr (1942) termed such species sympatric, and Gause (1934) pointed out that two species with identical ecology cannot persist together in the same area. Shannon's breeding site classification had two broad divisions, depressions in the ground and containers on or above the ground. The first was sub-divided into Natural (lakes, ponds, etc.) and Artificial (reservoirs, wells, etc.). The second was similarly sub-divided into Natural (tree-holes, leaf axils, etc.) and Artificial (domestic containers, etc.). A consideration of some of the species discussed here would indicate that this suggested relationship between habitats and the species found therein cannot be carried too far. For instance, the three aëdine species, *A. aegypti*, *A. apicoargenteus* and *A. simpsoni* are closely related, but in this study were found in widely different habitats. A further argument against a too rigid adherence to this postulation is that in West Africa *A. aegypti* is typically a domestic container breeder and *A. simpsoni* a leaf axil breeder, although in East Africa the former is also found breeding in tree-holes. The only genus in this area which obeys the postulated relationship at all closely is *Eretmapodites*, all the species of which have been taken from some kind of ground container.

When the factors which may determine the distribution of these species are considered, certain ecological gradients must be recognised within this area. Continuous readings of temperature and relative humidity taken in the village and forest showed that the latter area was typically cooler and more humid

than the village and that the micro-climate changed more slowly. Furthermore, in forest conditions the degree of organic contamination of the water increased. The larval habitats also underwent a physical change, in that those in the village typically presented large, exposed surface areas of water, while those in the forest were smaller and more concealed. Finally the food sources of the blood feeding females varied in the urban and forest environments, giving a range of hosts including man, other mammals, reptiles and birds.

It has been found in the laboratory (Surtees, 1958*b*) that egg-laying of *A. aegypti* is inhibited by small surface areas, deep containers and a high degree of organic contamination. These factors would serve to limit the breeding to the village area. It has also been found that egg-laying is more intense in dark and cool conditions, which would account for the majority of the breeding taking place inside houses. Furthermore, in this area *A. aegypti* is anthropophilic so that the concentration of the food of the female in the village would also serve to restrict the range of the species. A further point of interest is that, whilst *A. aegypti* was absent from the available natural habitats in the cocoa plantation, when clay pots were placed out it bred with greater intensity there than in any other areas beyond the village. Thus it would seem that a food source such as would be provided by workers in the cocoa plantation is as important as suitable breeding sites in deciding the local distribution of the species. Whilst similar laboratory studies to those mentioned above have yet to be carried out on the other species in this area, it may be suggested that such factors, combined with host availability, play their part in determining the distribution of the species. Previous results on feeding preferences indicate that host availability may play an important part in the distribution of mosquito species generally. *A. apicoargenteus* has been found to be a monkey biter (Haddow, 1952), and at Ilobi the breeding was concentrated in the forest at the higher levels, a fact which may suggest an arboreal animal as host. Davis and Philip (1931), using the precipitin test, found that the blood meals of *C. nebulosus* in this region gave a positive result for chicken and goats, and at Ilobi this species was most abundant in the scrub-zone, where there were always great numbers of domestic animals. Haddow (1952) found that *E. chrysogaster* was a monkey biter, and at Ilobi this species was largely restricted to the areas where monkeys were found.

The greatest problem presented by the results obtained from this study is that of the fluctuations in numbers of the species. Table III shows that these underwent a sharp decline in the middle of the rainy season. It would be expected that, with the abundance of water at this time, the mosquito population would be at a maximum. In the case of *A. aegypti* the initial build-up in numbers is thought to be due to the hatching of the drought resistant eggs which have survived the dry season until the beginning of the rains (Surtees, 1958*c*). With regard to the mid-year decline, it has been found in the laboratory that the greater the density of larvae per container, food and all other factors being controlled, the longer the developmental period and the higher the mortality Surtees (1959). It is therefore suggested that as the population builds up in the field the limits of the larval environment are reached, and increased larval mortalities result in a reduced population. In other words, a certain population maximum is reached where the food supply becomes so reduced that the larvae either die or take a longer time to reach the adult stage.

Summary

Mosquito investigations carried out in an isolated village in Southern Nigeria comprised a survey of the natural larval habitats and studies on the distribution and the seasonal incidence of the major species. It was found that *Aëdes aegypti* was largely restricted to domestic containers in the village, *A. longipalpis* to tree holes in the rain forest, *Eretmapodites chrysogaster* to cocoa husks in the cocoa plantation, *Harpagomyia taeniarostris* to leaf axils and *Eretmapodites pencillatus* to snail shells. Other species had a more plastic breeding pattern. A succession of species was shown to exist from the village, through scrub into the forest, consisting of *A. aegypti*, *A. apicoargenteus*, *Culex nebulosus*, *Megarhinus brevipalpis*, *E. chrysogaster*, *Culex albiventris*, *A. longipalpis* and *A. simulans*.

The numbers of larvae increased at the beginning of the rainy season, declined in the mid-rainy season (June and July) and built up again in August, before a final drop at the end of the rainy season.

The coincidence between the natural classification of breeding sites and the species found therein, as postulated by Shannon (1931), is discussed and is shown to hold for only a few of the species described here. The plasticity of breeding behaviour is discussed.

The pattern of distribution in this area is considered to be determined by a combination of factors, including those relating to the habitats of the larvae and the food sources of the adult females. It is further suggested that the mid-year drop in numbers is a population density reaction, because it was found that under controlled conditions the greater the density of larvae the higher the mortality and the longer the developmental period.

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THE GROWTH OF LARVAE AND THEIR CASES AND THE LIFE CYCLES OF FIVE SPECIES OF CADDIS FLIES (TRICHOPTERA)

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Introduction

Little work has been done on the growth of larval caddis flies. Nielsen (1942) made observations on the growth of several species of larvae from the springs of the Himmerlands in Denmark. The same author (1948) studied the increase in size of the larval cases of five species of Hydroptilidae and assumed that the growth of the larva took place parallel with that of the case. He also showed (1950) that in winter the growth of *Apatidea cimbrica* was reduced, despite the constant temperature of the spring water. Khalil (1953) studied the growth and life cycles of five species of caddis flies and Hanna (1957) of four species.

Apart from my work (1957*a*) on *Limnephilus politus* McLachlan and *L. marmoratus* Curtis, no comparison has been made of the relative growth rates of larvae and cases. I have therefore now made a comparative study of the growth of some caddis larvae and their cases, and have also studied their life cycles.

Material and Methods

The species studied, and the localities where they were collected, are listed below.

Limnephilidae :

Limnephilus flavicornis (F.).—Basingstoke canal, Fleet, Hants.

L. lunatus Curtis.—Basingstoke canal, Fleet, Hants.

Potamophylax stellatus (Curtis).—Stream from Blue pools running into River Pang near Bradfield Hall, Berks.

Sericostomatidae :

Brachycentrus subnubilus Curtis.—Whitewater River, Mattingly, Berks.

Rhyacophilidae :

Agapetus fuscipes Curtis.—Stream from Blue pools running into River Pang near Bradfield Hall, Berks.

The larvae of *P. stellatus* and *A. fuscipes* were collected from the lower reaches of the stream between May 1954 and September 1955. In October 1955 most of the stones were buried in sand owing to silting, and the number

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of larvae was greatly reduced. I was therefore obliged to collect upstream about 400 yards from the silted region for the rest of the period up to April 1956.

Samples of the population were taken at monthly intervals. No constant number was obtained but about one hundred larvae were collected each month. Pupae and adults were also collected when present.

Both larvae and their cases, after preservation in 70 per cent. alcohol, were measured wet to the nearest millimetre, by means of a binocular microscope fitted with a scaled eye piece. The larvae were pressed gently and measured from the anterior margin of the frontoclypeus to the posterior margin of the tenth abdominal segment.

All the species were studied for two years except *B. subnubilus*, which was studied only for 14 months.

Results

The measurements of larvae are illustrated in histograms (figs. 1–5); those of cases are also illustrated in histograms in an unpublished thesis (Hanna, 1956).

The larvae of *P. stellatus* and *A. fuscipes* were found in all months of the year; those of *L. flavicornis* and *L. lunatus* in all months except October. Larvae of *B. subnubilus* grew mainly in May and June. The rate of growth of *A. fuscipes* could not be determined because of an overlap of generations. However, the increase of the 5 mm. class from 22·4 to 56·5 per cent. and the 6 mm. class from 4 to 16·3 per cent. between 13th April and 12th May suggests that the larvae grew rapidly during this period. In all species studied there was little growth in winter. *L. flavicornis* and *L. lunatus* spent the winter months in the early larval stages. A small number of overwintering fully grown larvae and pupae of *P. stellatus* were found together with the early stages. A few pupae of *A. fuscipes* were also found in winter with larvae of all stadia. *B. subnubilus* passed the winter as growing and fully grown larvae.

Pupae of *L. flavicornis* and *L. lunatus* were obtained from early June to early October, while those of *B. subnubilus* were found from late March to mid-April. The pupae of *P. stellatus* were found in all months except June, as shown in the following table:

Table I.—*The monthly percentage of pupae of* P. stellatus

1954		1955		1955	
May	5·2	January	4	September	44
June	.	February	4·4	October	69
July	6·2	March	3·2	November	13·7
August	29·3	April	0·7	December	3·7
September	39·2	May	4·8	1956	
October	62·5	June	.	January	2·6
November	16·3	July	6·9	February	2·3
December	5·1	August	34·2	March	1·9
				April	1·8

The decline in the percentage of pupae of this species from 3·2 to 0·7 per cent. between March and April, 1955 suggests that overwintering pupae were

then giving rise to adults. A single adult female was taken on 13th April, 1955. The disappearance of overwintering larvae in May, 1955 suggests that those larvae had then pupated. This view was confirmed by the increase in the number of pupae from 0·7 per cent. to 4·8 per cent. from April to May. No pupae were found in June which suggests that these pupae had given rise

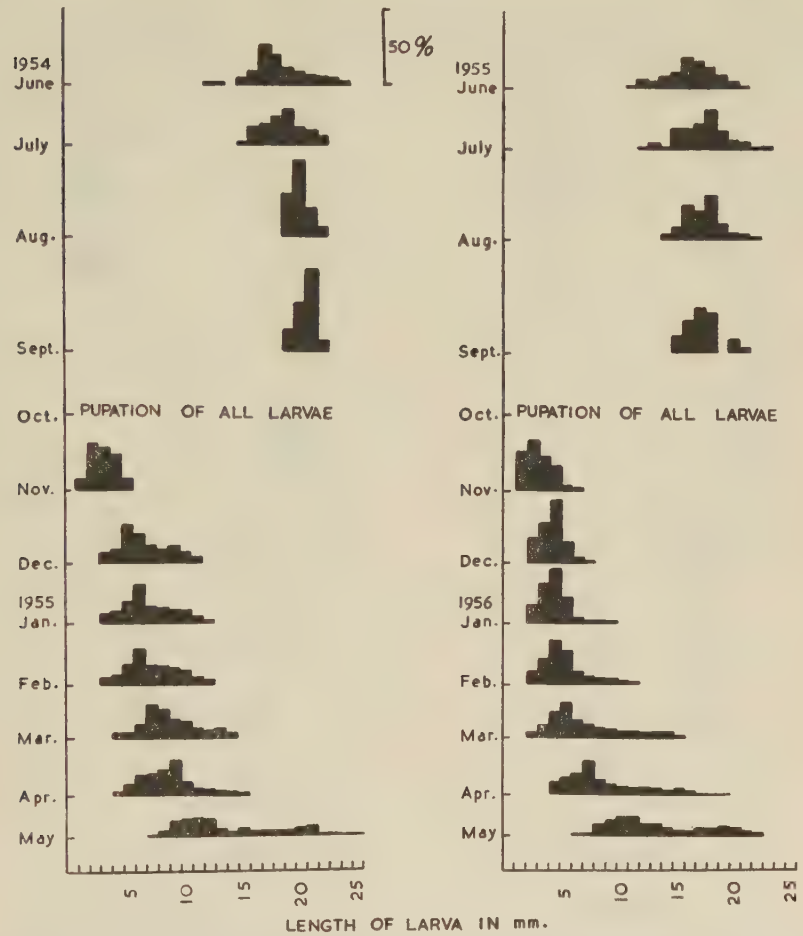

FIG. 1.—The monthly percentage of larvae of *Limnephilus flavicornis* (F.) in each millimetre length class.

to adults. The reappearance of pupae in July suggests that the larvae of the new generation had then started to pupate. Pupae of *Agapetus fuscipes* were found in all months of the year.

In the laboratory at room temperature the pupal period lasted 23 to 26 days for *L. flavicornis*, 19–23 days for *L. lunatus*, 21–24 days for *P. stellatus*, 16–18 days for *B. subnubilus* and 14–16 days for *A. fuscipes*.

The adults of *L. flavicornis*, *L. lunatus*, *P. stellatus* and *A. fuscipes* were always found resting on the vegetation during the daytime, whatever the

weather conditions, and only flew if disturbed. Those of *B. subnubilus* were seen to fly actively on warm sunny days, whereas on cloudy and cold days they were only found resting in sheltered places.

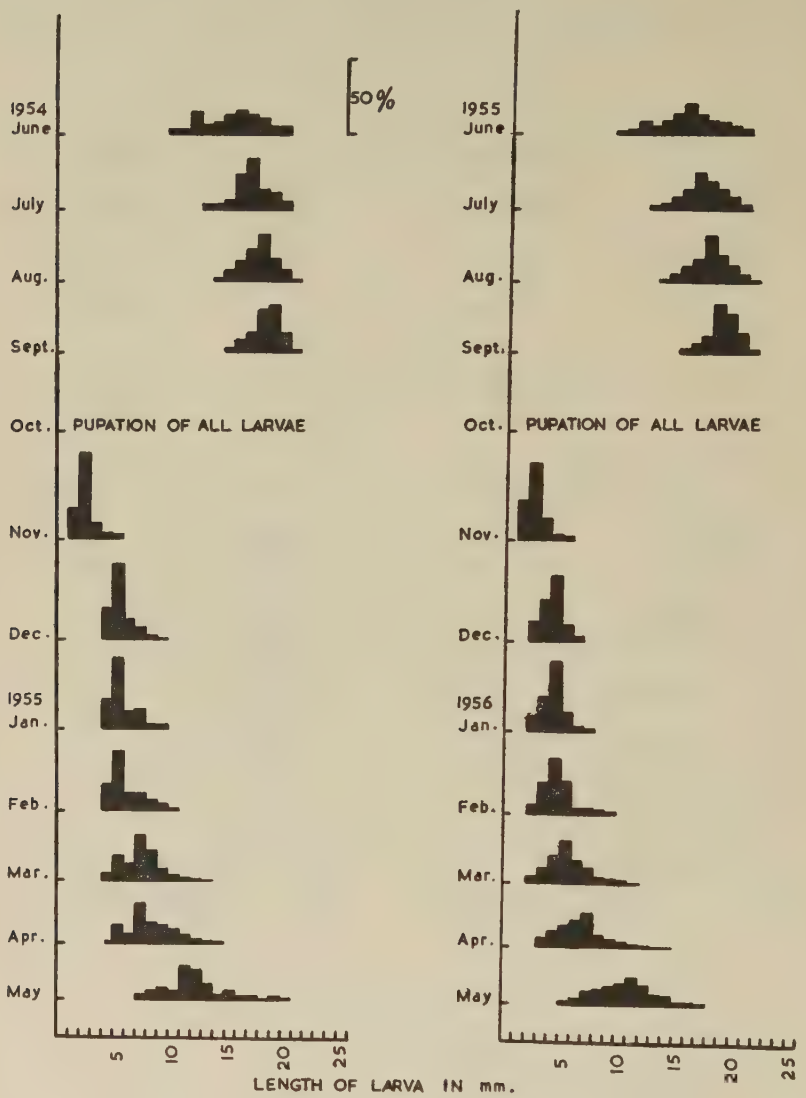

FIG. 2.—The monthly percentage of larvae of *Limnephilus lunatus* Curt. in each millimetre length class.

A few egg masses of *L. flavicornis* and *L. lunatus* were found in early September and in early October hundreds were found on the aerial part of the vegetation bordering the canal. A few egg masses of *L. lunatus*, however, were observed on vegetation just underneath the water surface. One egg mass of this species was found on a case of *L. flavicornis* on 7th March, 1956,

and the larvae were ready to hatch. The egg masses of *P. stellatus* were found in October and November on vegetation above the water surface and those of *B. subnubilus* were seen in very large numbers attached to the vegetation a few centimetres below the water surface.

Fig. 3.—The monthly percentage of larvae of *Potamophylax stellatus* (Curt.) in each millimetre length class.

There was only one generation a year in *L. flavicornis*, *L. lunatus*, *P. stellatus* and *B. subnubilus*. The life cycle of *A. fuscipes* could not be determined because of the overlap of generations.

In all species studied the increase in size of the case took place parallel with the growth of the larva.

Discussion

These observations show that there was little growth in winter, which suggests that its rate varies with temperature. Light and food may also play an important role. The larvae of *L. flavicornis*, *L. lunatus*, *P. stellatus* and *B. subnubilus* feed mainly on detritus, though large numbers of diatoms, desmids and chlorococcales were also included. In winter there may be a considerable reduction in the microflora and this may cause a decline in the rate of growth, as previously shown with *L. politus* and *L. marmoratus* (Hanna,

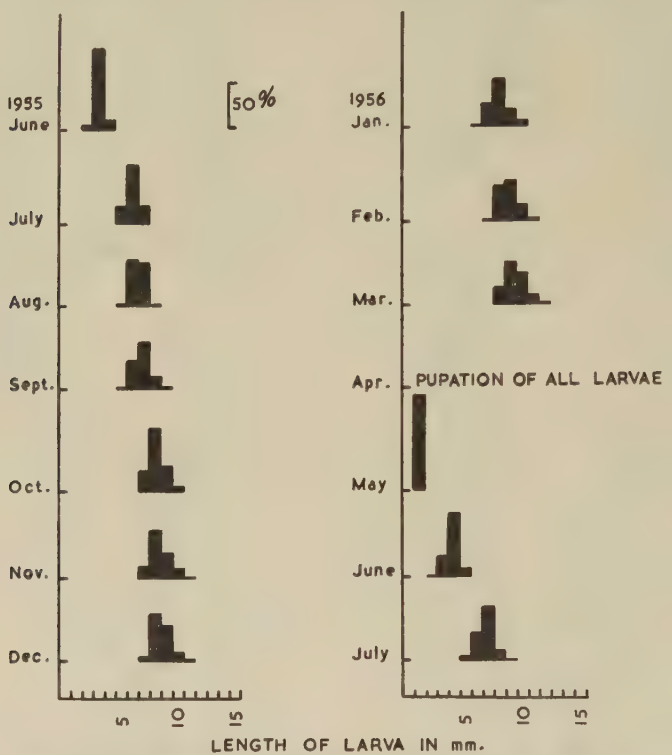

Fig. 4.—The monthly percentage of larvae of *Brachycentrus subnubilus* Curt. in each millimetre length class.

1957). After September, 1955, the larvae of *P. stellatus* and *A. fuscipes* were collected from the upper reaches of a stream at Bradfield, where the temperature remains around 10° C. in all months of the year. Despite this constant temperature there was a slow growth in winter, which suggests that light and food may be the governing factors in this part of the stream. In the lower reaches, where the larvae were collected from May 1954 to September 1955, the temperature fluctuates between 6·2° C. and 15° C.

The life cycles of *L. flavicornis*, *L. lunatus*, *P. stellatus* and *B. subnubilus* lasted one year, and there was only one generation. As stated above, the life cycle of *A. fuscipes* could not be determined on account of the overlap of generations and although I measured the larvae of this species to an accuracy of

0·5 mm. from May, 1955 to April, 1956 the generations could not be separated. As the larvae and their cases are generally equal in length, I feel it may be possible to study the life cycle if the cases are measured to an accuracy of 0·1 mm. Harker (1950, 1952) had the same difficulty in studying the life cycles of two species of *Baëtis* (Ephemeroptera).

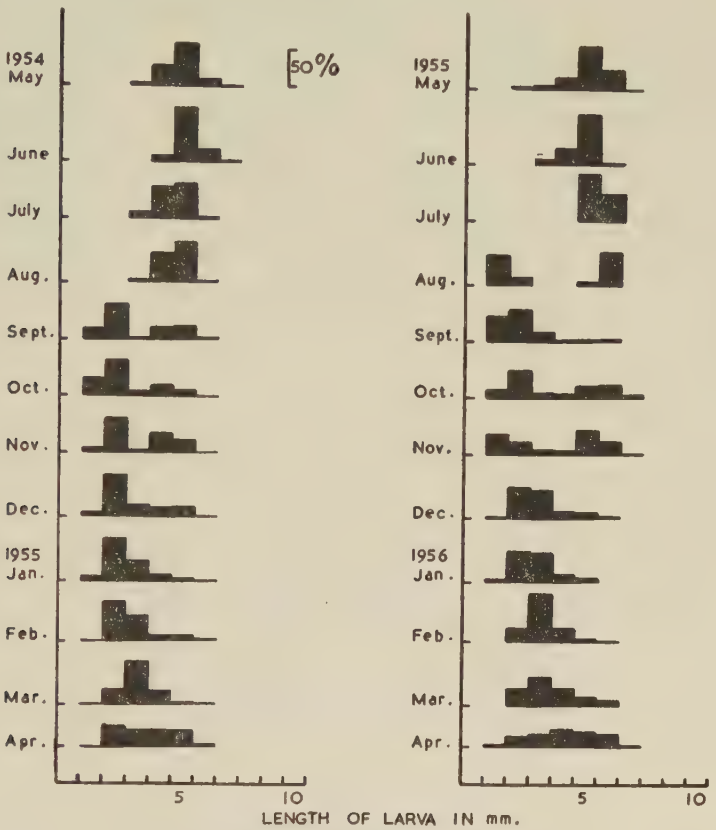

Fig. 5.—The monthly percentage of larvae of *Agapetus fuscipes* Curt. in each millimetre length class.

The main emergence of *L. flavicornis*, *L. lunatus* and *P. stellatus* was during autumn. Crichton (1956) found that many limnephilids emerged mainly in autumn at Wokefield in the Reading area and Mosely (1939) also recorded that many were autumnal.

B. subnubilus had a restricted flight in the latter part of April. It was also collected between 16th April and 2nd May over several years beside the Kennet canal near Reading (Crichton, Baker and Hanna, 1956).

A. fuscipes had a prolonged flight period and, except in January and February, the adults were always to be found. Nielsen (1942) records the swarming period of this species, in the springs of Himmerlands, from June to August, while he found it to be limited from late May to early June in the River Sussa in Denmark (1948*a*). Khalil (1953) found that adults emerged

from early May to mid-July in a stream in the Sheffield area.

Felber (1908) and Scheffler (1932) considered temperature as an important factor governing the life cycles of caddis flies. Ulmer (1925) showed that the number of generations was correlated with latitude and temperature. Marshall (1939) suggested that five of the species she collected from Lake Erie had two generations, but there was no evidence from larval collections. Milne (1943), however, recorded one generation only for three of these species.

From light trap collection of adults at one site near Reading, Crichton (1956) suggested that there might be overwintering fully grown larvae and pupae of *L. flavicornis* and *L. lunatus*, from which came the adults in spring and early summer. In the Basingstoke canal, where I made my monthly collections over a period of two years, I did not find overwintering fully grown larvae or pupae of these two species. However, I did collect a small number of fully grown larvae and pupae of *P. stellatus* in winter which would give rise to adults in spring and early summer. The occurrence of pupae in winter has been recorded by Siltala (1907) for *Oxyethira* sp., by Felber (1908) for *Acrophylax* sp. and *Cerebrus* sp., by Fisher (1932) for *Silo nigricornis* (Pictet), *S. pallipes* (F.) and *Goëra pilosa* (F.), and by Khalil (1953) for *Rhyacophila dorsalis* (Curtis).

The egg masses of *L. flavicornis*, *L. lunatus* and *P. stellatus* were found attached to vegetation above the water surface. I have found that the larvae of these three species hatched more quickly when they were submerged than when kept out of water. This agrees with Wesenberg-Lund's observations (1910) on *Glyphotaelius punctatolineatus* Retz. He found that, in dry periods, the development of the embryos was inhibited but in rainy periods they grew with a remarkable speed. This suggests that hatching of the larvae of these limnephilids depends to a large extent on rainfall. In dry seasons it is quite possible that it may be delayed and some of the egg masses may even over-winter and hatch in the following spring. Thus I have found an egg mass of *L. lunatus* on 7th March, 1956. In the Himmerlands in Denmark Nielsen (1942) suggested that *Anabolia nervosa* (Curtis) might over-winter in the egg stage.

Summary

The growth of the following five species of caddis larvae and their cases has been studied : *Limnephilus flavicornis* (F.), *L. lunatus* Curtis, *Potamophylax stellatus* (Curtis), *Brachycentrus subnubilus* Curtis and *Agapetus fuscipes* Curtis. It was found that increase in size of the case took place parallel with the growth of the larva. In all these species there was little growth in winter and it is suggested that the rate of growth varies with temperature, and that light and food may also have some effect.

There was only one generation in the year in *L. flavicornis*, *L. lunatus*, *P. stellatus* and *B. subnubilus*. The life cycle of *A. fuscipes* could not be determined because of the overlap of generations. The effect of rainfall on the hatching of larvae is discussed.

Acknowledgments

I am indebted to Dr. M. I. Crichton for his guidance and encouragement. I wish to express my gratitude to Professor A. Graham for accommodating me in his department, and to the Egyptian government for financial assistance while this work was in progress.

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A DESCRIPTION OF THE NYMPHS OF BRITISH *GERRIS* SPECIES (HEMIPTERA–HETEROPTERA)

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Mitis (1937) described the nymphs of the *Gerris* species of mid-Europe and constructed a key to species groups. Ecological work described elsewhere (Brinkhurst, 1958) required full identification of nymphs, and by reference to Mitis (1937) and Macan (1956) this proved possible. The following descriptions and key serve to identify at least late instar nymphs.

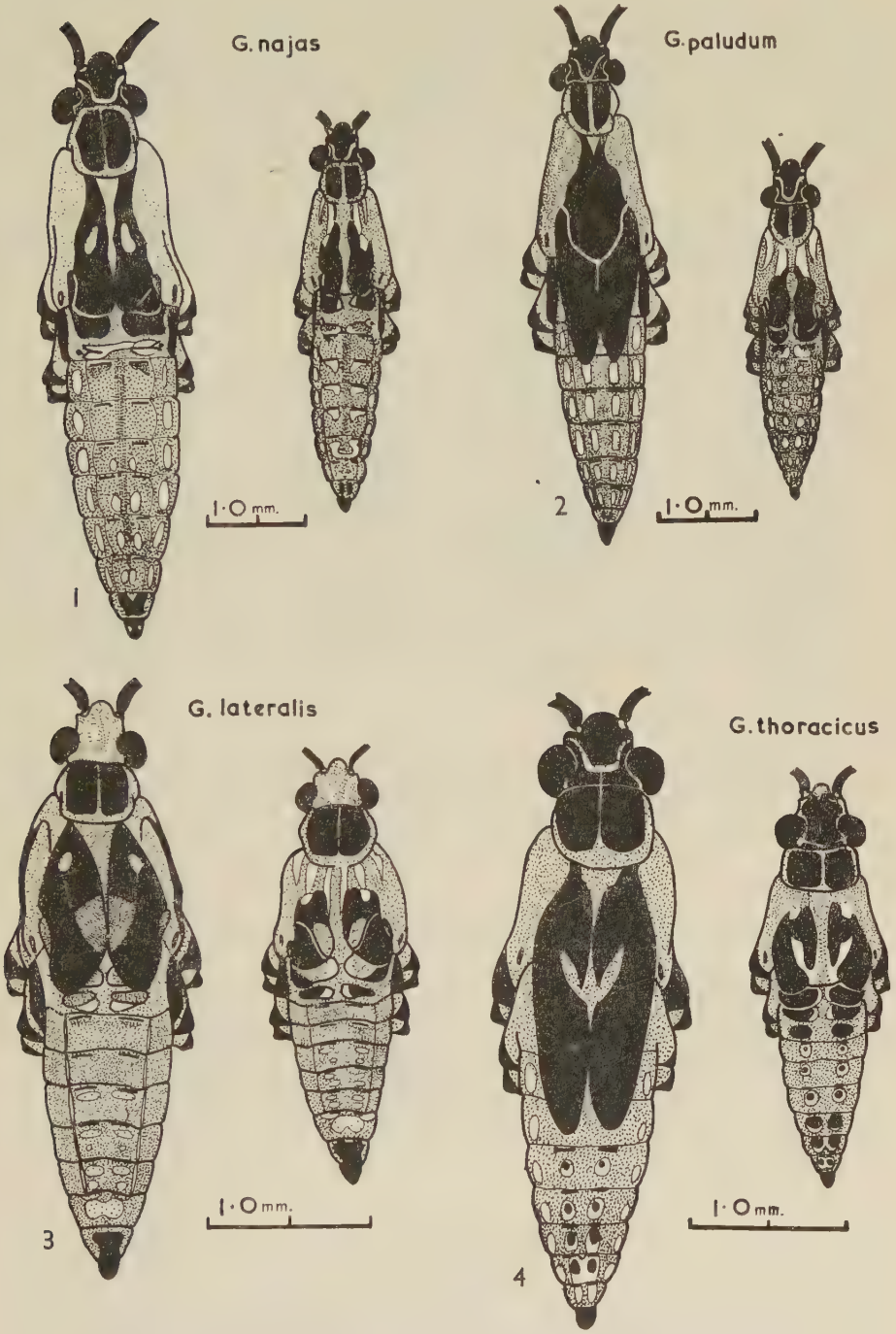
Methods

Nymphs were reared in the laboratory and collected from populations of a single species in the field. Whole mounts were drawn with the aid of a camera-lucida.

The lengths of the antennal and hind limb segments and the greatest breadth of the head were measured by means of an eye-piece micrometer, twenty-five individuals of each instar being used wherever material was sufficiently abundant. The overall length of the nymphs was not measured as this varied with the physiological state of the individual. There are intertergal and intersternal muscles, not present in the adult insect (Brinkhurst, 1958), which can bring about considerable telescoping of the abdominal segments. Sprague (1956), discussing this phenomenon in *Hydrometra martini* Kirkaldy, showed that the abdomen was periodically inflated both with air drawn into the gut prior to ecdysis, and with food.

Results

The diagnostic characters used in the key to nymphs are described separately for each species. The mesonotal marks consist of light patches on the distal end of the presumptive scutellum, separating this from the developing wing buds. There are other, more anterior, light marks on the mesonotum in some species (*najas*, *gibbifer*, *lateralis*, *lacustris*) marking the anterior end of the dark mesonotal patches in the fourth instar, which become enclosed within the more extensive dark marks in the fifth instar. The abdominal marks of most importance are those on terga 2–7, lying posterior to the transverse phragmatal pits which may themselves have light marks on their posterior borders. These marks are often supplemented by light patches in the centre of each laterotergite. The fore femoral patterns are like those described by Macan (1956) for adults, but are not so sharply defined and are somewhat variable. Figure 9 shows the commonest form of the pattern in fully developed fifth instar nymphs.



FIGS. 1–4. Fourth and fifth instar nymphs of: (1) *Gerris najas* Degeer; (2) *G. paludum* Fab.; (3) *G. lateralis* Schummel; (4) *G. thoracicus* Schummel.

The following key is designed to apply to fourth and fifth instar nymphs in particular, although, with practice, earlier instars are determinable. Adults or late instar nymphs are to be found from March to October, and if two species are present in a natural population this key, with the measurements given in Table I, should serve to distinguish between all instars if this is required.

G. najas Degeer

Large nymphs, antennal segment 1 larger than segments 2 and 3 together; principal mesonotal marks absent (fig. 1); abdominal marks white-yellow, oval, on terga 1–7, becoming less distinct or even absent on more anterior terga; fifth instar almost always apterous.

G. paludum F.

Large nymphs, antennal segments as above; light marks on mesonotum absent (fig. 2); abdominal marks white-yellow, oblong-oval, on terga 2–7; fifth instar with fully developed wing buds.

G. lateralis Schummel

Broad nymphs, but smaller than the above, with first antennal segment shorter than second and third together; mesonotal marks broad, almost uniting in the mid line (fig. 3); abdominal marks on segments 4–7 paired (sometimes single on tergum 4 of fifth instar), all marks dark yellow-brown, with darker markings red-brown not black as in other species; fore femora as in figure 9B, with a dark mark on upper surface almost covering the whole length, and covering one-third to half of ventral surface. (Described from rather few specimens.)

G. thoracicus Schummel

Antennal segments as for *G. lateralis*; mesonotal marks lanceolate, and confluent with a light streak in the mid line (fig. 4); abdominal tergal markings black with white-yellow borders on terga 4–8 in fifth instar, all terga in the fourth; laterotergal marks present in fifth instar.

G. costae H.S.

As *G. thoracicus* except that abdominal marks of fifth instar present on terga 5–8 only.

G. gibbifer Schummel

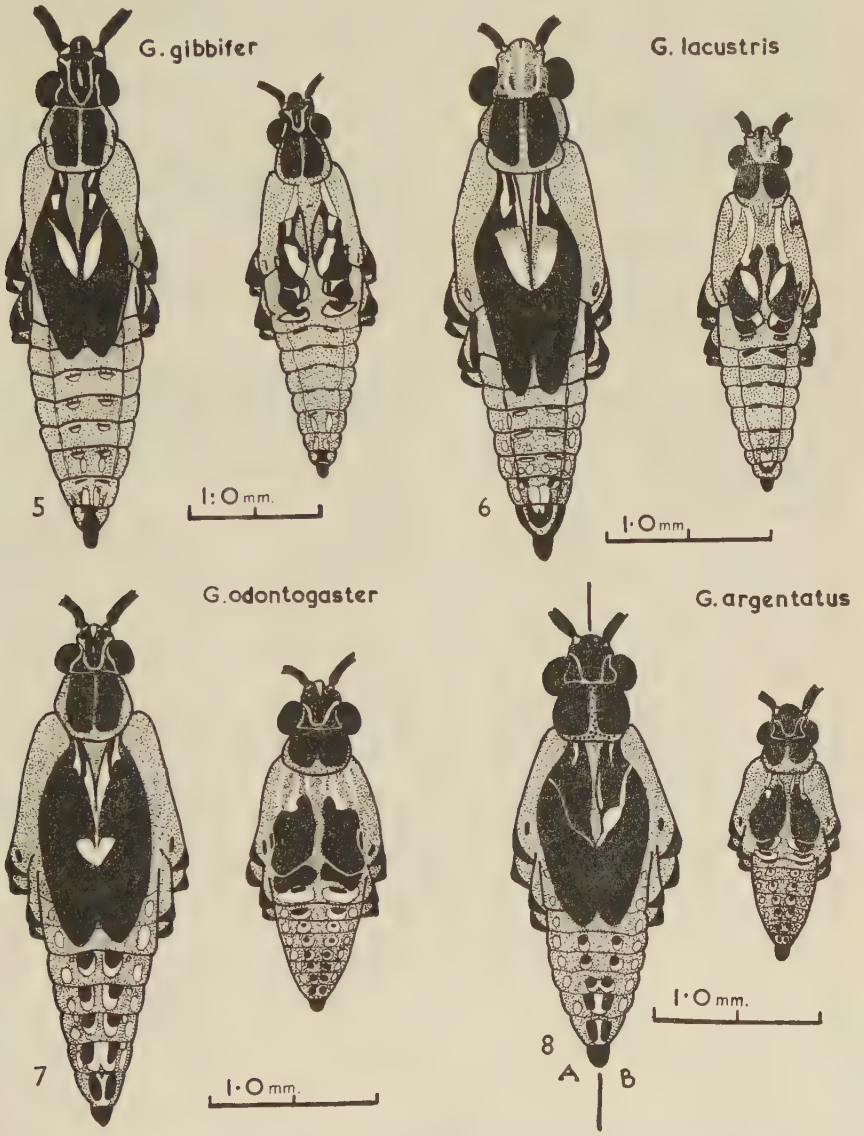
Antennal segments as in *G. lateralis*; mesonotal marks elongate-oval especially in fifth instar; abdominal marks on terga 6–7 only, with a dark spot on outer anterior margin of marks on tergum 7; an X-shaped dark mark visible on tergum 8 (fig. 5); fore femora as in figure 9C with a black band extending from tip to base of upper surface, completely or almost completely encircling the distal half, and a short band on the ventral surface extending from tip halfway to the base.

G. lacustris (L.)

Antennal segments as above; mesonotal marks broad, as in *G. gibbifer* (fig. 6); abdominal markings clear on terga 5–7 in fifth instar (6–7 on other instars), outstanding on 7, with light marks on latero-tergites on segments 4–7; dark markings on eighth tergum W-shaped; fore femora with dark markings extending from tip to two-thirds way to the base on upper surface, and from tip to one-third of way to the base on lower surface (fig. 9A).

G. odontogaster Zetterstedt

Antennal segments as above; mesonotal marks forming a broad V-shaped mark (fig. 7); abdominal markings on terga 1–8 black, with a white border more prominent posteriorly; white marks present on laterotergites; fore femora as in figure 9D, with a broad band on upper side running from distal end to two-thirds way to the base, sometimes extending on to lower surface. A larger species than *G. argentatus* which it resembles, full measurements being given in Table I.



FIGS. 5–8.—Fourth and fifth instar nymphs of: (5) *Gerris gibbifer* Schummel; (6) *G. lacustris* L.; (7) *G. odontogaster* Zetterstedt; (8) *G. argentatus* Schummel. (A–B, two alternative colour patterns).

TABLE I.—*Lengths of antennal and hind limb segments and breadth of head in seven* Gerris *species*

Species	Instar	Breadth of head	Antennal segments				Hind limb		
			1	2	3	4	Femur	Tibia	Tarsus
G. paludum	2	0·79± —	0·36± —	0·23± —	0·23± —	0·54± —	1·60± —	1·00± —	0·73± —
	3	0·97±0·03	0·58±0·02	0·31±0·02	0·34±0·01	0·69±0·03	2·90±0·10	1·60±0·01	0·90±0·05
	4	1·30±0·08	1·02±0·04	0·51±0·02	0·50±0·02	0·86±0·02	4·80±0·20	2·70±0·10	1·20±0·04
	5	1·70±0·08	1·80±0·09	0·78±0·04	0·71±0·04	1·02±0·03	8·03±0·24	4·80±0·25	1·86±0·11
G. najas	1	0·59±0·03	0·25±0·01	0·17±0·01	0·25±0·02	0·46±0·02	1·50±0·09	0·90±0·06	0·53±0·04
	2	0·84±0·06	0·41±0·02	0·25±0·02	0·31±0·03	0·56±0·03	2·40±0·08	1·40±0·06	0·70±0·06
	3	1·10±0·05	0·71±0·04	0·36±0·02	0·41±0·02	0·69±0·03	3·90±0·10	2·20±0·09	0·86±0·05
	4	1·30±0·08	1·30±0·10	0·56±0·03	0·63±0·05	0·83±0·05	5·70±0·21	3·60±0·20	1·20±0·04
	5	1·70±0·09	2·10±0·14	0·86±0·08	0·86±0·05	0·99±0·04	8·00±0·30	5·50±0·31	1·60±0·11
G. lacustris	1	0·51±0·04	0·16±0·03	0·09±0·01	0·09±0·01	0·35±0·03	0·60±0·05	0·46±0·03	0·40±0·05
	2	0·58±0·05	0·21±0·03	0·12±0·00	0·13±0·02	0·43±0·04	1·00±0·07	0·60±0·04	0·46±0·06
	3	0·78±0·05	0·35±0·02	0·18±0·02	0·20±0·01	0·50±0·06	1·70±0·10	0·93±0·06	0·66±0·04
	4	1·00±0·05	0·56±0·03	0·33±0·01	0·33±0·02	0·71±0·04	2·70±0·13	1·40±0·07	0·83±0·06
	5	1·20±0·03	0·89±0·06	0·49±0·02	0·46±0·03	0·87±0·06	4·20±0·16	2·20±0·15	1·30±0·07
G. gibbifer	4	1·40±0·04	0·73±0·05	0·41±0·03	0·43±0·03	0·84±0·04	3·40±0·06	1·80±0·07	1·20±0·66
	5	1·50±0·04	0·99±0·02	0·58±0·04	0·54±0·04	0·96±0·03	4·40±0·12	2·50±0·03	1·50±0·12
G. odontogaster	4	1·00±0·02	0·58±0·02	0·35±0·02	0·35±0·01	0·76±0·03	2·50±0·08	1·30±0·08	0·83±0·07
	5	1·20±0·07	0·87±0·04	0·49±0·04	0·46±0·02	0·87±0·04	3·70±0·17	2·00±0·13	1·10±0·02
G. argentatus	4	0·82± —	0·36± —	0·27± —	0·26± —	0·64± —	2·00± —	1·00± —	0·60± —
	5	1·00± —	0·70± —	0·41± —	0·41± —	0·70± —	3·10± —	1·50± —	0·87± —
G. thoracicus	3	0·86±0·04	0·36±0·02	0·20±0·01	0·20±0·01	0·54±0·02	1·60±0·03	0·93±0·02	0·60±0·03
	4	1·10±0·06	0·63±0·05	0·35±0·02	0·33±0·04	0·68±0·04	2·50±0·07	1·40±0·04	0·90±0·06
	5	1·50±0·11	0·91±0·05	0·49±0·05	0·49±0·04	0·56±0·05	4·00±0·11	2·30±0·13	1·40±0·08

G. argentatus Schummel

Antennal segments as above ; mesonotal marks absent in 50 per cent. of individuals, small and oval in other 50 per cent. ; abdominal marks as in *G. odontogaster* (fig. 8) ; fore femora as in figure 9E, with a black band running from tip to two-thirds way to the base, along anterior edge and extending on to ventral surfaces. Smaller than the above species, full measurements being given in Table I.

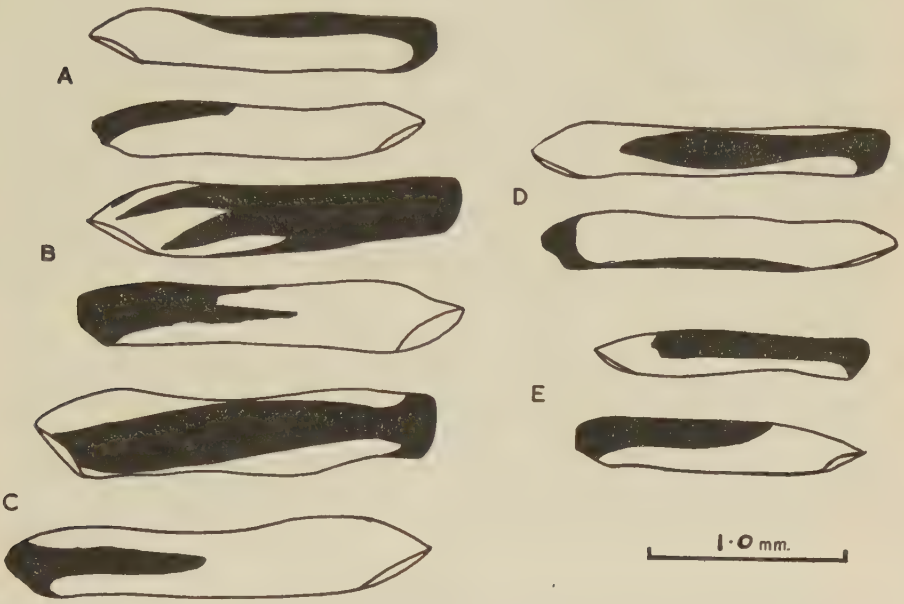


FIG. 9.—Markings of fore femora of fifth instar nymphs of *Gerris* species, drawn to scale. For each species the dorsal view is shown above the ventral view. A, *lacustris* ; B, *lateralis* ; C. *gibbifer* ; D, *odontogaster* ; E, *argentatus*.

The following key has been constructed for the separation of the British *Gerris* species, and is based on the above descriptions. Confirmatory evidence of identification may be obtained by reference to Table I. The habitat notes are derived from observations detailed elsewhere (Brinkhurst, 1958).

KEY TO THE FOURTH AND FIFTH INSTAR NYMPHS OF THE BRITISH *Gerris* SPP.

(See Table I for measurements)

– Large nymphs, no mesonotal marks, antennal segment 1 longer than 2 + 3 together 1
– Smaller nymphs, mesonotal marks nearly always present, antennal segment as long as or shorter than 2 + 3 together 2
1 Apterous, abdominal marks oval on terga 4–7 in fifth instar (fig. 1). *On rivers* . . . . . **G. najas** Degeer
– Macropterous (adults possibly brachypterous), abdominal marks oblong-oval on terga 2–7 (fig. 2). *On lakes or large ponds in the south-east of Britain* . . . . . **G. paludum** Fabricius

2 Abdominal marks dark brown-black with white surrounds (figs. 4, 7, 8) 3
– Abdominal marks brown-yellow to white without surrounds (figs. 3, 5, 6) 6
3 Mesonotal marks absent or very small (figs. 7, 8) 4
– Mesonotal marks elongate-crescentic (fig. 4) 5
4 Mesonotal marks absent in 50 per cent. of fifth instars, small as in *G. odontogaster* in the others (fig. 8); fore-femora as in fig. 9E. A small species. *Common in Phragmites* . . . **G. argentatus** Schummel
– Mesonotal marks a small broad V (fig. 7); fore femora as in figure 9D. A larger species. *On ponds* . . . . . **G. odontogaster** Zetterstedt
5 5–6 pairs median abdominal marks in fifth instar (fig. 4). *On brackish water* . . . . . **G. thoracicus** Schummel
– 3-4 pairs of median abdominal marks in fifth instar. *On mountain pools in the north and west of Britain* . . **G. costae** Herrich–Schaeffer
6 Mesonotal and abdominal marks dark brown (fig. 3); fore-femora as in fig. 9B. Often apterous, rare . . . . . **G. lateralis** Schummel
– Mesonotal and abdominal marks yellow-white; fore-femora as in fig. 9A or C. Rarely apterous, common 7
7 Mesonotal marks broad, abdominal marks on laterotergites and median terga, very distinct on terga 7; dark marks on terga 8 W-shaped. Slightly smaller than *G. gibbifer* (Table I) (fig. 6); fore femora as in figure 9A. *Very common on ponds as well as other habitats* **G. lacustris** L.
– Mesonotal marks elongate-oval, white abdominal marks not so outstanding and absent from laterotergites except the last in instar 5; dark marks on terga 8 X-shaped (fig. 5); fore femora as in fig. 9C. Slightly larger than *G. lacustris* (Table I). *Common on lowland peat pools and dykes in England and Wales* . . . . **G. gibbifer** Schummel

Acknowledgments

This work formed part of a thesis submitted for the Ph.D. degree in the University of London, the work being financed by a Nature Conservancy Studentship.

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THE SOURCE OF THE SUBSTANCE PRODUCED BY A QUEEN HONEY-BEE (*APIS MELLIFERA* L.) WHICH INHIBITS DEVELOPMENT OF THE OVARIES OF THE WORKERS OF HER COLONY

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Introduction

Development of the ovaries of the worker bees of a colony is normally inhibited by a substance produced by the queen and distributed over her body surface, from which the workers obtain it (de Groot and Voogd, 1954; Butler, 1956). This inhibitory substance is particularly abundant on the queen's head (de Groot and Voogd, 1954); the same or an analogous substance is produced in the queen's mandibular glands, from which it is distributed over her body, and this normally inhibits the workers of her colony from rearing further queens (Butler and Simpson, 1958). An experiment has now been made to determine whether the substance that inhibits ovary development in worker bees is also produced in the mandibular glands of the queen.

Experimental Technique

Thirty-six well-ventilated Perspex cages, each 60 × 50 × 90 mm. high, were used. Each cage was supplied continuously with distilled water and pollen-candy (prepared by mixing icing sugar with 20 per cent. by weight of fresh bee-collected pollen and sufficient distilled water to make a stiff paste). Fifteen worker bees, 1–3 days old, from a colony headed by a mated laying queen, and 15 worker bees of the same age group from a similar colony, were placed together in each cage.

A piece of comb, 5 cm. long × 2 cm. wide, consisting entirely of empty worker cells, was placed in each cage for the bees to cluster upon.

The cages were divided into three groups of 12. The body of a mated queen honey-bee which had been extracted in ethanol in a Soxhlet apparatus for 32 hr. was attached with a loop of wire to the top of the comb in each of the cages in one of the control groups. In each of the cages of the experimental group a similarly extracted queen was attached to the comb, but, at the beginning of the experiment, and every third day afterwards, each of the queens was dipped into a solution in 20·0 ml. ethanol of the contents of the mandibular glands of 12 mated laying queens freshly killed by freezing. Each time a queen was dipped in this way her body retained approximately 0·15 ml. of the solution. The cages forming the second control group had no queens attached to their pieces of comb. All the cages of bees were kept together in an incubator at approximately 32° C.

This experiment began on 6th August, 1958 and ended on 22nd August, when all the bees were killed and their bodies preserved in Pampel's fluid. Later, 25 bees from each cage were taken at random and their ovaries examined to see whether or not they had developed.

Results and Conclusions

The results obtained are shown in Table I.

Comparison by the "*t* test" shows that the difference in ovary development between the bees in the cages of the control group "A" and that of the bees

in the other control group " B ", is just significant at the 5 per cent. level, but this result, if not accidental, is not relevant to the present problem. The

TABLE I.—*Degree of ovary development in control and experimental cages*

Group A — No queen attached to comb; no mandibular gland contents given		Group B — Fully-extracted queen attached to comb; no mandibular gland contents given		Group C — Fully-extracted queen + mandibular gland contents attached to comb	
Cage No.	No. bees showing ovary development	Cage No.	No. bees showing ovary development	Cage No.	No. bees showing ovary development
1	17	13	22	25	9
2	22	14	18	26	4
3	16	15	23	27	6
4	16	16	21	28	11
5	21	17	20	29	8
6	19	18	21	30	5
7	19	19	16	31	4
8	21	20	21	32	0
9	19	21	21	33	9
10	18	22	21	34	4
11	18	23	21	35	0
12	17	24	20	36	7
Total=	223	Total=	245	Total=	67

degree of ovary development of the bees in the cages of the experimental group " C ", to which the mandibular gland contents of mated queens were given, was very significantly reduced compared with either of the control groups " A " and " B " ($P < 0{\cdot}001$ in each case). It seems clear, therefore, that the substance on the body surface of a queen honey-bee that inhibits development of the ovaries of her workers is produced in her mandibular glands. Thus, both a substance that inhibits queen rearing by worker honey-bees (Butler and Simpson, 1958) and one that inhibits development of their ovaries are produced in the mandibular glands of the queen honey-bee. It is, of course, possible that one controlling substance only is involved, but at present there is no evidence on the point.

Presumably the secretion of a queen's mandibular glands becomes distributed over her body surface, and obtainable by the workers, when she grooms herself.

SUMMARY

The contents of the mandibular glands of a mated queen honey-bee can inhibit development of the ovaries of a group of queenless worker honey-bees.

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THE GROWTH STAGES OF *ARIXENIA* (DERMAPTERA)

By J. L. Cloudsley-Thompson

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My paper on the growth stages of *Arixenia esau* Jordan and *A. jacobsoni* Burr (Cloudsley-Thompson, 1957) raised a number of questions. One of these has since been answered by Lord Medway (1958), who has confirmed the parasitic nature of the relationship between *A. esau* and its host, the Hairless Bulldog Bat, *Cheiromeles torquatus* Horsf. Medway's experiments show that *Arixenia* feeds upon the epidermal products of the bat, but will also attack and eat injured insects, including members of its own species. No mention is made of *A. jacobsoni* in the Niah Cave, Sarawak, but Lord Medway tells me (*in litt.*) that the Free-tailed Bat, *Tardaridus mops* (de Blainv.) is not found there. Both species of *Arixenia* were present in the collection from a hollow tree in Selangor, Malaya, which formed the subject of my paper and it may well be, as suggested, that *A. esau* is a parasite of *C. torquatus* whilst *A. jacobsoni* occurs chiefly on *T. mops*.

Although only four nymphal instars were present in the Malayan material, the smallest specimens were so large and so heavily chitinised that I supposed there must actually be five nymphal stages and that first instar nymphs were absent from the collection. I suggested, as an explanation, that they might be free-living and hide away in crevices. In this I was wrong, for shortly afterwards Mr. Tom Harrisson, the Curator of the Sarawak Museum, was kind enough to send me two pregnant female *Arixenia esau* from the Niah Cave which he and Lord Medway had collected. On dissection one of them was found to contain five large embryos, the other four well developed nymphs, confirming that the insects are ovoviviparous. This may be related to the parasitic habit: *Arixenia* and Hippoboscidae would appear to be among the few exceptions to the general rule that parasitic organisms show prolific reproduction. But in these insects viviparity, although inevitably correlated with lowered fecundity, results nevertheless in reduced mortality of the young (Cloudsley-Thompson, 1955).

Since the embryos were not fully developed it was difficult to assess their head widths, but these appeared to average about 2·0 mm. Those of the four nymphs measured 2·0, 2·0, 2·2 and 2·3 mm. and fall well within the range observed in the Malayan specimens, of which the mean head width of the smallest instar was 2·30 mm.

Mr. W. H. Potts has made the interesting suggestion that a short-lived first instar may be passed in the body of the female, the young hatching during their true second instar. From the growth ratio calculated for *A. esau*, the head widths of such first instar nymphs might be expected to average about 1·95 mm. (Cloudsley-Thompson, 1957). In view of the head widths of the embryos mentioned above, I do not think this can be the case, although it is not impossible.

It must therefore be concluded that *Arixenia esau* probably has four nymphal instars, not five as previously suggested, and the same is probably true of *A. jacobsoni*.

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Book Notices

Physiology of insect development. Edited by Frank L. Campbell. 8vo. Chicago (University of Chicago Press), 1959. Pp. xiv + 167 : text illust. (*The Developmental Biology Conference Series*, 1956). £1 10*s*. 0*d*.

This is one of ten volumes recording the results of the Developmental Biology Conference, which took place in 1956 under the auspices of the National Academy of Sciences, Washington. It deals with the conference on Insect Physiology held at Macdonald College.

The voices of the participants were recorded on magnetic tape during the Conference and the material afterwards re-dictated and amended, and the results published in dialogue form.

There are six sections, two of which deal with embryology and the remainder with larval development and tissue culture, metamorphosis and diapause, histolysis and tumors, and regeneration, respectively. A selected bibliography completes the volume.

Key to the Names of British Butterflies and Moths. By R. D. Macleod. 8vo. London (Pitman), 1959. Pp. vii + 86. 15*s*.

This useful work giving the origin and meaning of the scientific and common names of British butterflies and moths is the first of its kind to be published for over a century.

There are three sections—an introductory one (11 pages) in which the author discusses and analyses the form and origin of scientific names, a list of scientific names (pp. 15–76) and a shorter list of common names (pp. 77–86) with their derivation and meaning. Each list is divided into three sections—Butterflies, Macro-moths and Micro-moths, with the names in alphabetical order.

THE LONGEVITY OF WORKER HONEY BEES (*APIS MELLIFERA*)

By J. B. Free and Yvette Spencer-Booth

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Introduction

Surprisingly little is known about the length of life of worker honeybees. Different estimates, especially of the mean during spring and summer, vary considerably—6–10 weeks in summer (Phillips, 1939), 5–7 weeks in midsummer (Wedmore, 1942), not over 12 weeks in summer and not over 4–6 weeks during nectar flows (Root *et al.*, 1945), 5–6 during spring and summer (Park, 1949).

A knowledge of the mean longevity of bees emerging at different times of the year is of practical importance in managing colonies so that they reach their maximum foraging strengths at times coinciding with the main nectar flows, and the present work was undertaken to determine this.

Method

Four healthy colonies (A, B, C and D) of hybrid Italian bees were used. Every Saturday from 23rd March to 5th October, 1957 a group of 100 bees, which had emerged during the previous 24 hours from combs placed in an incubator, were introduced to each colony. The combs from which the bees emerged were taken from various colonies, no attempt being made to select one strain. Bees of each group were marked with paint of the same colour to distinguish them from the bees of other groups and from marked bees already in the colonies. They were not anaesthetised during marking.

Every Sunday, after flying had ceased, the entrances to the hives were closed. The variously marked bees were counted the next morning, the colonies being manipulated in such a way as to reduce to a minimum the number of marked bees which flew. After counts on 7th October the colonies were not examined again until 28th March of the following year; thereafter they were examined at intervals until all the marked bees had disappeared.

Marked bees were regarded as one day old when introduced and consequently three days old when first counted in the colonies. Since the colonies were examined at weekly intervals, data were obtained on the number of bees of the various groups which were alive when 10, 17 and 24 days old, and so on. The number of bees of a group lost from one week to the next were assumed to have died at a mean age of three and a half days older than their age when last counted.

It was realised that some of the newly emerged bees might meet with a hostile reception by the bees of the recipient colony, and that some of them might crawl or be dragged out of the hive entrance and become lost. It was therefore originally intended to calculate the longevity of a group from the number of its members successfully introduced, *i.e.* the number of them counted two days after introduction.

However, it was found that a mean of 23·5 per cent. of the bees present when three days old had disappeared before they were ten days old, and 17·8

per cent. of the bees present when ten days old had disappeared before they were 17 days old. It is most unlikely that the performance of some duty within the hive was the cause of the high death rate, particularly since the death rate was higher in the first week than in the second. It seems reasonable to assume that most of the losses were caused by inadvertent damage during marking, the injured bees being unable to return to their hive when they left it on their orientation flights.

Ribbands (1952) recorded the ages at which 99 marked bees (47 emerged in April and 52 in June) first foraged and when they were last observed to do so. The youngest bee to forage was nine days old, and the youngest age at which a bee was last seen was when it was 17 days old, most bees being observed until they were considerably older. In the results quoted below, therefore, the longevity of the bees has been calculated from the number of those present when 17 days old, it being assumed that any bees foraging before that age were still surviving. This method obviously tends to give an over-estimate of longevity, since some bees were probably lost before they were 17 days old as a result of causes other than damage during marking.

Results

Longevity of Bees Emerging in Spring and Summer

The mean longevity of bees emerging at different times, as calculated by the above method, is shown in figure 1, of all the bees emerging in the same

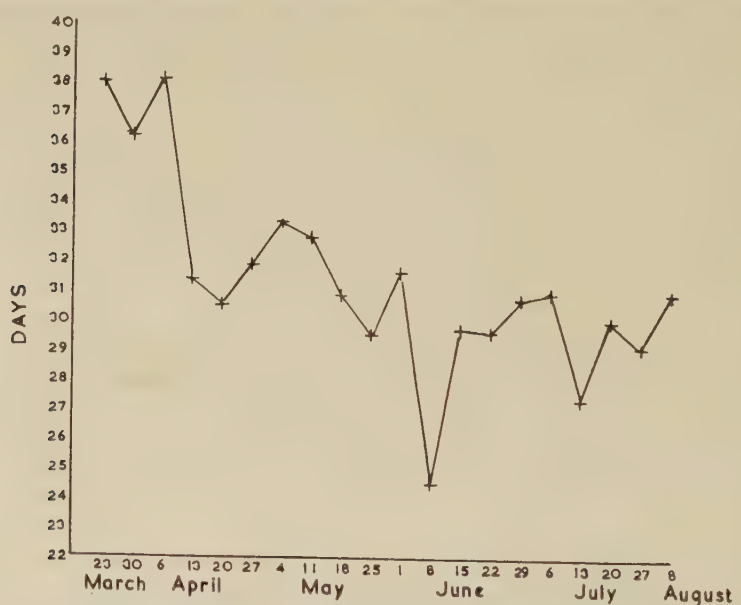

Fig. 1.—Mean longevity of bees emerging at various times during spring and summer.

calendar month in Table I. Although it varied considerably in consecutive weeks, its mean monthly value diminished steadily until June.

TABLE I.—*Longevity (days) of bees at various times of the year in different colonies (data for August are for bees introduced on 3rd August only)*

	Month of emergence					
Colony	March	April	May	June	July	August
A	40·7	38·7	32·3	32·2	31·3	35·6
B	36·5	29·3	31·2	28·7	28·9	29·8
C	36·3	31·1	30·5	26·8	27·6	29·0
D	35·4	35·3	32·1	28·2	29·2	29·1
Mean all colonies	37·1	33·0	31·6	28·6	29·3	30·9

The percentage of bees surviving at different ages is given in figure 2, all the bees which emerged during the same calendar month being considered together. The percentage of bees emerging in August which survived for longer than indicated is not known, since the last bees to be marked in August were only 39 days old when they were last counted before winter. The percentage given for September is the mean percentage of the bees introduced on 7th and 14th September which were present in the colonies when they were 24 days old.

From March to June there was a general decrease in the percentage of bees surviving at all ages, followed by a general increase in August and September. The maximum ages attained by bees emerging in the various months were: March, 67 days; April, 60 days; May, June and July, 53 days.

The percentage survival from week to week is given in figure 3. In general the weekly death rate at all ages increased from March to June. Bees emerging in July had a slightly lower death rate than those emerging in June, and bees emerging in August had, in general, a lower death rate than those emerging in any other month.

Queen cells were removed from Colony A on 17th and 24th June, 8th, 15th, 22nd and 29th July, and 5th and 12th August. This colony had less brood than the other colonies and it was not so evenly distributed over the brood area of the combs. The colony was requeened on 13th August. In all months the mean longevity of bees in colony A was greater than that in any of the other colonies (Table I) and, in general, their weekly survival rate was also greater at all ages (Table II).

TABLE II.—*Percentage survival of bees present the previous week in colony A and in colonies B, C and D*

	Month of emergence											
	March		April		May		June		July		August	
Colony:	A	B, C & D	A	B, C & D	A	B, C & D	A	B, C & D	A	B, C & D	A	B, C, & D
Age of bees (days)												
24	86·4	81·0	78·4	72·1	77·3	78·5	71·4	63·1	72·7	64·9	88·0	82·7
31	84·2	75·4	82·4	68·1	55·3	52·0	69·1	40·5	65·0	44·8	68·5	75·5
38	61·8	60·0	72·0	53·2	59·1	32·8	51·4	18·6	39·2	29·0	69·3	85·1
45	63·8	61·7	38·9	27·1	14·7	6·6	16·7	19·2	25·0	22·2	.	.
52	70·0	16·3	42·9	34·4	30·0	0	55·6	20·0	0	20·0	.	.
59	23·8	26·7	0	9·1	0	.	0	0	.	0	.	.
66	40·0	0	.	0	.	.	.	.	.	.	.	.

Longevity of Bees Surviving the Winter

Bees of nine age groups (emerging between 10th August and 5th October) were present in the colonies when they were examined on 7th October. Only two bees which emerged on 10th August were counted and neither of these survived the winter. The percentages of the bees of the remaining groups present on 28th March of the following year and on subsequent examinations is shown in Table III. The percentages of the different groups which survived the winter did not vary in accordance with the age of the groups concerned.

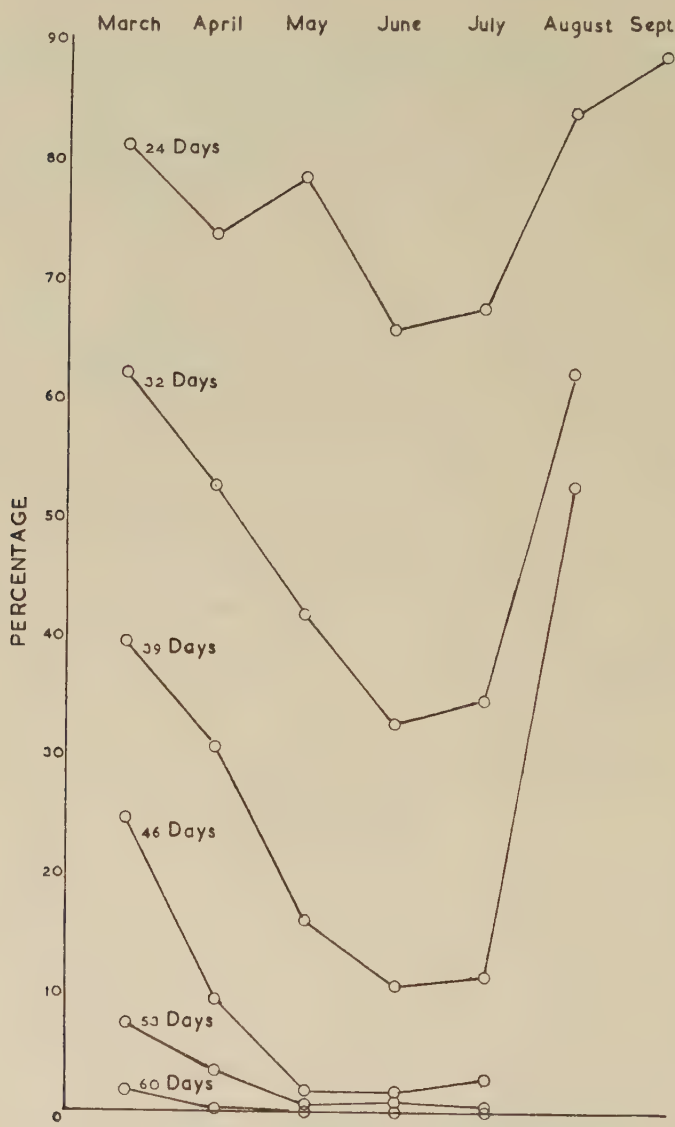

Fig. 2.—Percentage of bees surviving at different ages.

The reasons for the marked variations that did occur—comparatively low percentages of bees introduced on 24th August and 14th September survived—are unknown.

The percentages of bees alive on the first examination in spring (28th March) and which were present on subsequent examinations are also given in Table III. During the spring and early summer the death rates of the over-wintered bees were about the same irrespective of their ages, with the

Fig. 3.—Percentage survival of bees present preceding week.

TABLE III.—*Survival of overwintered bees*

Date marked bees introduced	Number present when 17 days old	Number present 7 Oct.	% present 7 Oct.	% present surviving	Date colonies examined: 28 Mar.	3 April	17 April	25 April	1 May	9 May	16 May	22 May	Ju
17.viii	242	54	22·3	7.x	31·5	27·8	18·5	20·4	11·1	11·1	1·8	5·6	0
				28.iii		88·2	58·8	64·7	35·3	35·3	5·9	17·6	0
24.viii	212	85	40·1	7.x	11·8	11·8	11·8	9·4	2·4	0	0	0	0
				28.iii		100·0	100·0	80·0	20·0	0	0	0	0
31.viii	209	148	70·8	7.x	40·5	40·5	33·8	28·4	16·2	10·1	4·7	1·3	0
				28.iii		100·0	83·3	70·0	40·0	25·0	11·7	3·3	0
7.ix	243	221	90·9	7.x	44·1	34·4	29·4	26·7	16·3	11·3	5·9	2·3	0
				28.iii		77·6	66·3	60·2	36·7	25·5	13·3	5·1	0
14.ix	197	149	75·6	7.x	16·8	16·8	16·8	8·7	4·0	2·7	1·3	0	0
				28.iii		100·0	100·0	52·0	24·0	16·0	8·0	0	0
21.ix	259	259	100·0	7.x	40·2	38·6	25·1	19·3	15·1	12·4	5·0	1·5	0
				28.iii		96·2	62·5	48·1	37·5	30·8	12·5	3·8	0
28.ix	Not known	322	.	7.x	31·4	30·1	23·0	17·1	10·9	6·8	1·6	1·6	0
				28.iii		96·0	73·2	54·5	34·7	21·8	5·0	5·0	0
5.x	Not known	362	.	7.x	49·2	47·0	40·3	38·1	25·7	21·3	14·4	6·6	0
				28.iii		95·5	82·0	77·5	52·2	43·3	29·2	13·5	0

exception of the last group to be introduced the previous autumn (on 5th October), which in general had a lower death rate than the other groups.

The percentage of those marked bees present on 7th October which survived the winter differed markedly between the four colonies, about twice the percentage surviving in colonies C and D as in colony B, but the survival of the bees during the spring and early summer was about the same in each colony (Table IV).

TABLE IV.—*Survival of overwintered bees in the different colonies*

Colony	No. marked bees present: 7 Oct.	28 Mar.	% of bees present on 7 Oct. surviving on 28 March	% of bees present on 28 March surviving: 3 April	17 April	25 April	1 Mar.	9 Mar.	16 Mar.	22 Mar.	2 June
A	379	118	31·1	86·4	67·8	72·9	50·0	35·6	17·8	10·2	0·9
B	463	109	23·6	99·1	79·8	78·0	49·5	34·9	16·5	11·0	0
C	424	197	46·5	100·0	82·7	55·3	28·4	24·4	9·1	2·5	0
D	336	163	48·5	89·6	70·6	58·9	44·2	32·5	22·1	8·6	0

Discussion and Conclusions

The present technique undoubtedly gives the relative longevity of bees reared at various times of the year. The above results could be criticised on the grounds that marking itself adversely affects longevity, or that some of the paint marks became eradicated and a false impression of longevity was consequently obtained. However, the longevity of bees surviving the winter was about the same as that found when techniques not involving the use of marked bees were employed (Root and Root, 1920)—*see later*—and it is unlikely that marking adversely affects bees during the summer and not during the winter.

Furthermore, if marking were harmful one would suppose that bees given

two paint marks would, in general, die earlier than those given only one. Bees which were introduced on 4th, 11th and 25th May, 13th July, 14th and 21st September, and 5th October were marked with separate colours on the thorax and abdomen. The data presented in figure 1 and Table III show that the longevity of these bees was not abnormally different from that of bees given single marks on relative neighbouring weeks. Also, if paint marks became eradicated to a notable extent proportionately fewer bees with two marks would have been counted.

Langstroth (1866) requeened a colony with a queen whose worker progeny were of a different colour from those already present and observed that the last of the original workers disappeared three months later. In many subsequent statements on the longevity of bees there seems to be a confusion of the relationship between the mean length of life of workers and the maximum period to which some survive. Thus Riley (1893) states that at midsummer workers "do not average an individual life of more than three months". Wright (1926) noted that since the immature stages of workers occupy three weeks, Langstroth's bees which were present three months after their queen was removed must have lived ten weeks as adults. He assumed they were nurse bees for two of these weeks and foragers for the remaining eight. Further, assuming that the mean length of life of foragers in general was half that of these particular bees, he concluded that bees have a mean foraging life of four weeks which, in addition to the two weeks spent as nurse bees, made six weeks altogether.

As pointed out earlier, the present results may well give an over-estimate of the longevity of bees but, even so, the mean longevity of workers in spring and summer has been found to be considerably lower than previously supposed, although these findings do not in fact conflict with such previous results as are available. Thus Rösch (1925) gives figures for the maximum length of life in summer which are in general lower than those recorded in the present study, and Maurizio (1950) found the maximum length of life of summer bees in one experiment to be only 38 days and in another 31 days. Rockstein (1950) introduced 2,700 marked newly emerged bees to a colony. He removed 176 and found that only 11 remained 51 days after introduction. Ribbands (1952) recorded the ages at which marked bees were last seen to fly and calculated that in one experiment their mean longevity was 33·6 days and in a second experiment 34·8 days. Morland (1938) stated that during the active season of the year marked bees seldom lived more than 45 days, and their expectation of life seemed to be nearer to three weeks.

It is well known that in summer queenless bees live much longer than bees in normal queenright colonies (*e.g.* Anderson, 1931). Maurizio (1950) supposed that the duration of a bee's life is regulated to a very large extent by the amount of pollen consumed and the amount of brood rearing undertaken. She showed that bees in a broodless colony take on the physiological characteristics of winter bees and live much longer than those in normal colonies. Their fat-bodies are much more developed than those of bees in a colony with brood and they also live much longer; their pharyngeal glands remain developed when those of bees of equivalent age in a colony with brood have regressed. There is often a reduction in the amount of brood produced in colonies preparing to swarm (Simpson, 1959) so that physiological changes, similar to those mentioned

above, in the bees belonging to the colony in the present work which was rearing queen cells (colony A) could account for their greater expectation of life at all ages compared with bees of the other colonies.

However, Ribbands (1952) found that the greater the age at which bees began to forage the greater was their total duration of life, although their foraging life was less. Foraging therefore appears to be a more arduous occupation as well as probably a more hazardous one than nursing, although the latter also has an effect in reducing longevity. Foraging is diminished in colonies preparing to swarm (Ribbands, 1951), and this is probably also the case in broodless colonies, so the increased longevity of bees in such colonies may primarily be a consequence of a reduced foraging activity.

It has been shown in the present work that bees reared in spring have a greater expectation of life than those reared in midsummer, when the survival rate at all ages is lower. The worker population of a colony normally reaches its maximum in June or July (Jeffree, 1955) and consequently the ratio of brood to bees must have become reduced by then (*see* Simpson, 1959), so the low longevity of bees emerging in midsummer was not due to an increase in the amount of brood rearing undertaken by them. Probably, therefore, these bees began foraging earlier in life and foraged more consistently than those reared earlier in the year, with a resulting adverse effect on their longevity. August bees lived much longer than July bees ; the amount of brood produced in colonies declines rapidly during August in England (Simpson, 1959), but there is also normally far less forage available in August than in July.

There was no correlation between the ages of the bees emerging in August and September which were present at the onset of winter and the percentage of them surviving to the following spring, neither was their subsequent death rate during spring and early summer in accordance with their age. These observations are in agreement with those of Farrar (1943) that similar proportions of bees of various ages die in a broodless colony during winter. However, it has been found that overwintered bees which emerged during the first week in October had a greater longevity than those emerging in August and September. Evenius (1937) introduced marked bees to a colony in August and October and found that the former died earlier in the spring.

In the present study some of the bees emerging in August and September survived until late May, and a few of those emerging in the first week of October survived until the following June. The longest-lived bees survived over 217 days but less than 228 days. Root and Root (1920) found that if a colony is requeened in August with a queen whose progeny are of a recognizably different strain from the workers already present, some of the latter will be found in the colony until the following May, their date of disappearance depending on the amount of brood present in the colony. Farrar (1949) found that a few over-wintered bees lived for as long as 320 days in colonies which did not begin to rear brood until mid-June.

Differences in the amount of brood to be reared may have resulted in the marked differences in the percentage of bees surviving the winter in different colonies in the present investigation. However, other factors such as differences in colony size, the metabolic activity of the bees and the cluster temperature maintained by them, may also have had an effect (*see* Free and Spencer-Booth, 1958).

It is often stated that bees of some strains live longer than those of others (*e.g.* Root and Root, 1920 ; Wedmore, 1942), but adequate evidence to support these statements appears to be lacking. Any difference between strains would be very difficult to demonstrate conclusively owing to the large variations in the longevity both between workers of different colonies and between workers emerging on different weeks in the same colony.

Summary

1. A group of 100 marked worker honeybees was introduced into each of four colonies at weekly intervals from 22nd March to 5th October and their longevity ascertained.

2. The longevity of bees in spring and summer was found to be generally lower than previously supposed. It decreased in accordance with their date of emergence from early spring to midsummer, bees emerging in March living a mean period of just over five weeks and those emerging in June a mean period of about four weeks, the weekly death rate at all ages being greater in midsummer than at any other time.

3. The weekly death rate of bees emerging in August was considerably lower than that of bees emerging in the previous three months, and many of them survived the winter.

4. In the case of bees emerging in August and September there was no correlation between the ages of those present at the onset of winter and the percentage which survived to the following spring ; neither was their survival in the following spring and early summer correlated with their ages, bees of most groups being present at the end of May. But bees emerging in the first week of October had a lower death rate in the following spring and summer than the older bees present.

5. There were marked variations in the longevity of bees of different colonies, both during summer and winter.

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A STUDY OF LARVAL GROWTH, THE NUMBER OF INSTARS AND SEXUAL DIFFERENTIATION IN THE CHIRONOMIDAE (DIPTERA).

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Introduction

The dipterous family Chironomidae is a rather neglected group of insects and there is particular scope for systematic and biological work on the larval phases of the life histories. As a preliminary to an ecological study of certain of these larvae, an examination was made of the number of larval instars characteristic of the family, and of methods by which these instars could be recognised.

Edwards (1925), in his discussion of the phylogeny of the Nematocera, states that the Chironomidae have reduced the number of instars to four. This generalisation was probably based on the work of Pause (1918) who demonstrated four larval instars in *Chironomus thummi* Kieff., and Branch (1923 *a* and *b*) who found the same number in *C. cristatus* Fabr. and *Tanytarsus fatigans* Joh. Sadler (1935) subsequently showed that *Chironomus tentans* Fabr. also possesses four larval instars, and Rempel (1936) has demonstrated four in a species which Thienemann (1954) has named *C. rempelii* Thien. These species all belong to the subfamily Chironominae and little work has been undertaken on the other major subfamilies found in fresh water, the Orthocladiinae, Tanypodinae and Diamesinae.

The work on the orthocladiines has resulted in some confusion. Thus Kettisch (1936/37) measured the breadth of a number of head capsules of *Cricotopus trifasciatus* (Panz.) and stated that there are seven larval instars in this species. Berg (1950), on the other hand, measured the lengths of the head capsule in *C. elegans* Joh. and found no more than four instars. Thienemann (1954) expressed the belief that the observations of Pause and Sadler permit a generalisation to be made, and that four larval instars will be found to occur universally in the Chironomidae. One of the original aims of the work described in this paper was to test Thienemann's generalisation.

Methods

The recognition of insect instars is usually based upon the measurement of the width or the length of the head capsule (Dyar, 1890). This procedure was rejected in the case of the chironomid species investigated, as the compression caused by mounting the head capsules for microscopical examination resulted in considerable alteration in their dimensions. As an alternative, various structures within the head capsule were selected as parameters for determining the instars. Measurements were made before and after mounting to ensure that the structure selected did not undergo distortion.

In the species belonging to the subfamilies Orthocladiinae and Diamesinae the length of the labium was measured, *i.e.* the length from the posterior

ventral border of the head capsule to the tip of the foremost tooth of the labium (fig. 1, A). The teeth of the labium often become worn and blunted in full-grown larvae but with the scale of measurement being used the error involved was negligible.

In the mainly carnivorous subfamily Tanypodinae the rigid labium is replaced by a mobile epilabium which may lie in a variety of positions in fixed specimens. Therefore other structures had to be selected for measurement. Three species of this subfamily were examined, *Procladius choreus* (Meigen),

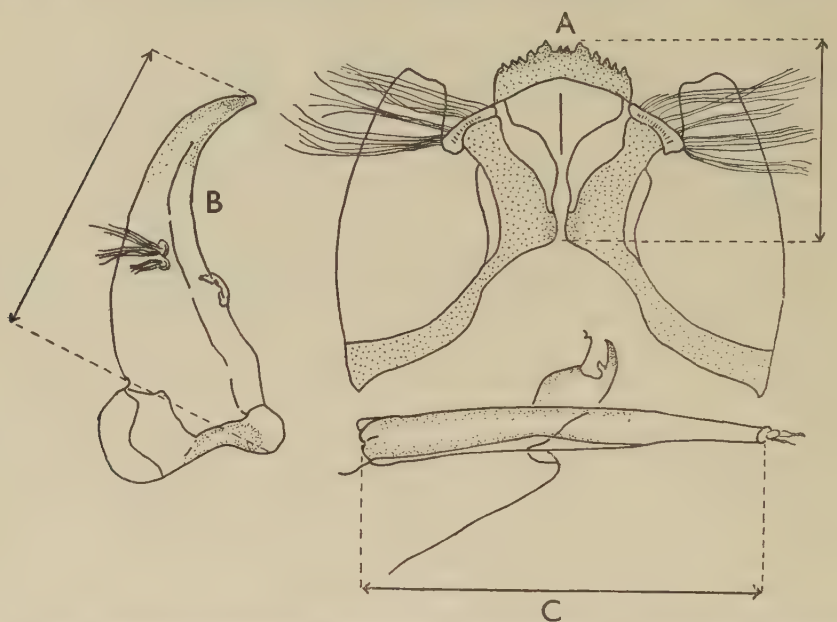

FIG. 1.—Structures measured in the separation of larval instars : A, labium of *Prodiamesa olivacea* ; B, mandible of *Anatopynia trifascipennis* ; C, antenna of *Clinotanypus nervosus*. (The antenna in C is shown partially retracted into the head capsule. Below the antenna is the side of the head capsule and above is the characteristically hooked mandible of this species.) Measurements were made between the two points indicated by the broken lines. The distance measured is indicated by the arrow in each case.

Anatopynia trifascipennis (Zett.) and *Clinotanypus nervosus* (Meigen). The mandibles of *P. choreus* and *A. trifascipennis* were found to be the most useful structures for measurement (fig. 1, B). In the case of C. *nervosus*, however, the mandible is a peculiar hooked structure (fig. 1, C) and the unusually long first segment of the retractile antenna proved to be a better parameter (fig. 1, C). The very small terminal segments were excluded from the measurements, since their growth rate differed from that of the majority of head structures (see below) and they were frequently lost in preserved material.

Dyar's Rule

Dyar's rule has been shown to be widely applicable in the Arthropoda (Dyar, 1890 ; Teissier, 1936). It provides a useful estimate of the dimensions

of the head capsules of instars which have not been found in the field. There have been few attempts to apply Dyar's rule to chironomid larvae and the results are rather contradictory. Rempel (1936) measured the widths of the labia of the four instars of *Chironomus rempelii* and stated that the species conformed to Dyar's rule, having a rate of growth (r) equal to 1·8. On the other hand, Berg (1950) measured the length of the head capsule in 166 specimens of the orthocladiine *Cricotopus elegans* and came to the conclusion that Dyar's rule was not obeyed. The values of r calculated from the mean lengths of the head capsules of each instar were 1·62, 1·52 and 1·43 respectively.

MacDonald (1956) assumed that the two tanypodine species which he studied possessed four instars and that their growth complied with Dyar's rule. He collected their third and fourth instars and obtained values of r which were used to calculate the dimensions of the missing first and second instars. He later obtained a few second instar individuals of *Tanypus guttatipennis* Goetgh. which agreed with the estimated value of their head size.

Results

(1) *Subfamily Diamesinae*

(a) *Prodiamesa olivacea* (Meigen)

The larval stages of this species were reared from eggs obtained in the field. Four larval instars were reared and figure 2 shows a histogram of the

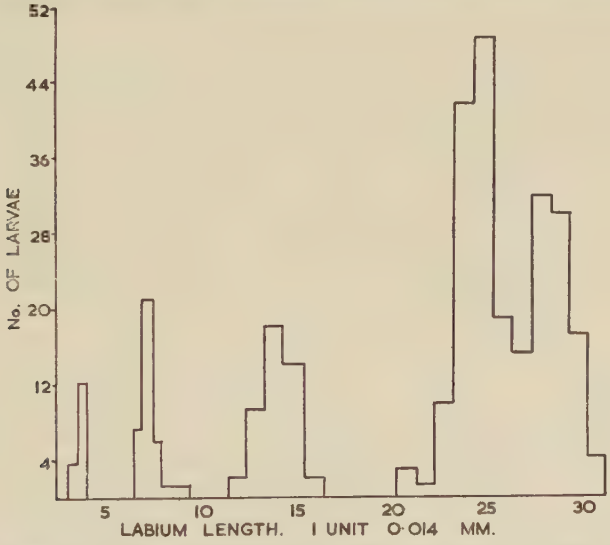

Fig. 2.—Histogram of the measurements made of the labia in the four instars of *Prodiamesa olivacea*.

measurements of the larval labium of each instar. The units of length are arbitrary units obtained from the scale on the micrometer eyepiece used in the microscope ; in this case one unit is equal to 0·014 mm. Measurements were made to the nearest unit in the case of the third and fourth instar larvae and to the nearest 0·5 of a unit in the case of the smaller larvae. These measure-

ments showed that the growth of the larval head capsules in this species conforms to Dyar's rule with a value of r equal to 1·9 (Table I). This value is calculated from the mean length of the labium in each instar.

TABLE I.

	Instars			
	1st	2nd	3rd	4th
Observed mean length of labium . .	3·90	7·50	14·10	26·34
Estimated mean length of labium . .	3·90	7·41	14·08	26·75

($r = 1·9$) (1 unit = 0·014 mm.)

The application of Dyar's rule is not entirely satisfactory, since the last instar group appears to show two clearly defined peaks. Analysis of this apparently bimodal distribution was facilitated by the use of arithmetic

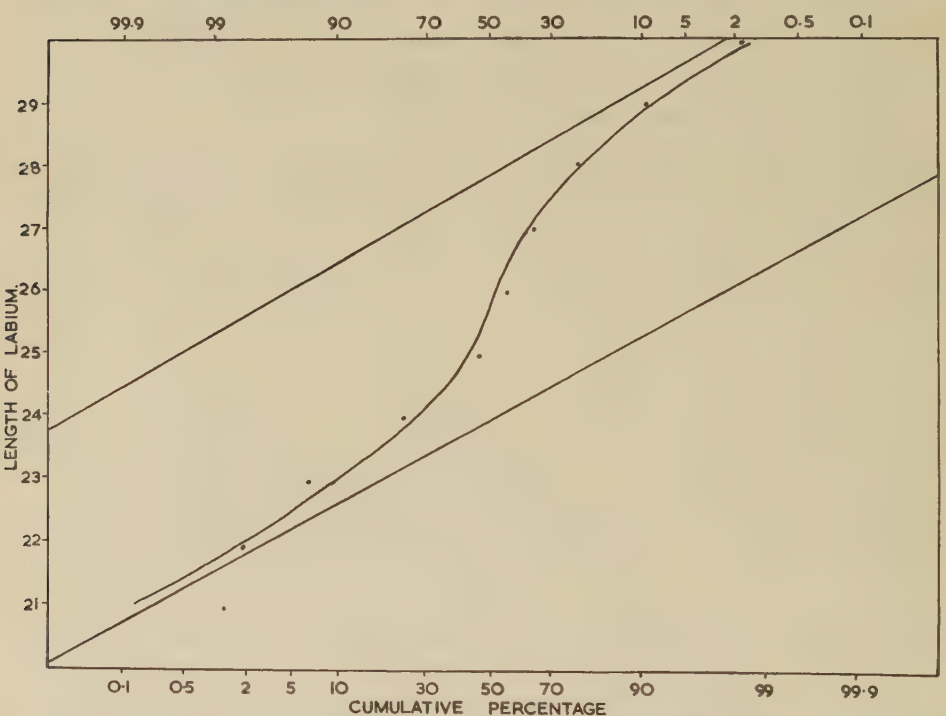

FIG. 3.—Lengths of the labia of last instar larvae of *Prodiamesa olivacea*, plotted on arithmetic probability paper. (The measurements are plotted as dots; the sigmoid curve is the resultant of the two straight lines which have been fitted.)

probability paper (Harding, 1949). A sigmoid graph was obtained on the probability paper (fig. 3) which showed that the fourth instar of *P. olivacea* has two distinct normally distributed components, and it appeared possible that these represented the two sexes, already differentiated at this stage. To test this, isolated last instar larvae were reared to emergence and the sex of

each imago noted. Fifty-four individuals were successfully reared and the labium length of each of the fourth instar larval exuviae was measured. The results (Table II) indicate that the sexes are already separated in the last larval instar.

TABLE II.—*Sexual differences in the length of the labium of last instar larvae of* Prodiamesa olivacea.

	Theoretical measurements (From probability paper)	Observed measurements (Reared larvae)
Modal length of labium . .	24—small size population	24—♂♂
	28—large size population	28—♀♀
Range in length of labium . .	21–27·8—small size population	22–27—♂♂
	24–30—large size population	24–30—♀♀

The point of inflection of the sigmoid curve occurs at the 50 per cent. level, indicating a 1 : 1 sex ratio in this species. The distinction between the sexes is apparent only in the last instar larvae. The labium of the third instar larvae were remeasured at a higher magnification, but the measurements gave no indication of a bimodal distribution.

Sexual differences are even more obvious in the pupae. Twenty-one male and twenty female pupal exuviae were mounted and their lengths measured. The mean length was 8·49 mm. in the case of the males, and 9·87 mm. in the females. Student's t test showed a very highly significant difference ($p < 0{\cdot}001$) between these means. There is also a more obvious morphological difference between the sexes in the pupal stage. The antennal coverings of the pupae are very long in the much smaller male, and relatively small in the female. This sexual distinction in the pupae was noted in a large number of chironomid species. It is probably common to the whole family since the very long antennae are a distinguishing feature of the male adult fly.

(2) *Subfamily Tanypodinae*

(a) *Clinotanypus nervosus* (Meigen)

The four instars of this species were collected in the field. Dyar's rule was applied to the measurements made on the first antennal segment (fig. 1, c), and the value of r was estimated to be 1·82 (Table III).

TABLE III

	Instars			
	1st	2nd	3rd	4th
Observed mean length of first antennal segment	7·50	15·00	28·22	50·74
Estimated mean length of first antennal segment	8·46	15·40	28·03	51·01

($r = 1{\cdot}82$) (1 unit = 0·0038 mm.)

Only one of the 321 individuals used in the measurements was in the first instar. This probably accounts for the rather poor agreement between the observed and the estimated antennal length for this stage.

The measurements of the last instar group were plotted on arithmetic probability paper and a bimodal distribution was again demonstrated. The two populations of last instar larvae were closely overlapping, with theoretical ranges for the length of the first antennal segment of 45·5–61 and 40–55 respectively. The theoretical modes occur at 53 and 47·5 units. Not so many last instar larvae of *Clinotanypus nervosus* as of *Prodiamesa olivacea* were reared to pupation. Nevertheless, in each case the larvae belonging to the large size group gave rise to female pupae and flies, and it may be assumed, therefore, that this species also shows a separation of the sexes in the last larval stage. Once again the graph drawn on probability paper indicated a 1 : 1 sex ratio.

The antennae of *C. nervosus* provide a good illustration of allometric growth in the Chironomidae. The very small terminal segments of the antennae are relatively long in the first instar, or larvula, and they form a progressively smaller proportion of the total antennal length in each subsequent instar. (Figure 1, c shows the relative proportions in the last instar.) In Table IV Dyar's rule has been applied to these terminal segments of the antennae.

TABLE IV

	Instars			
	1st	2nd	3rd	4th
Observed mean length of terminal segments of antennae	9·50	11·00	12·50	14·00
Estimated mean length of terminal segments of antennae	9·96	11·16	12·50	14·00

(1 unit = 0·0038 mm.)

The value of r upon which the estimated measurements are based is 1·12, but the value for the basal segment was shown to be 1·82 (Table III). Thus a change in proportion in the antennae during the larval life is clearly demonstrated. This has also been noted in other species and may be quite a general phenomenon in the Chironomidae. It is most obvious in the first instar, where the relatively long terminal segments are quite striking. Dorier (1933) figured the antennae of the larvula and larva of *Psectrocladius obvius* Walk. and described the differences in their proportions as being one of the morphological distinctions separating the first from the remaining larval instars. Quite possibly in the case of *P. obvius*, as in that of *Clinotanypus nervosus*, the change in proportion is a progressive change at each moult rather than an abrupt change at the end of the first instar.

(b) *Anatopynia trifascipennis* (Zetterstedt)

Measurements were made on the mandibles of 410 larvae of this species, belonging to the second, third and fourth instars. The existence of four instars is assumed, first instar larvae never having been taken in the field. The measurements conform to Dyar's rule with an estimated value of r equal to 1·8 (Table V).

TABLE V

	Instars			
	1st	2nd	3rd	4th
Observed mean length of mandible . . .		13·00	24·00	42·59
Estimated mean length of mandible . .	7·37	13·27	23·89	43·00

($r = 1·8$) (1 unit = 0·0038 mm.)

The last instar again shows indications of a bimodal distribution, although it is less clearly defined than in the species discussed above. The graph on arithmetic probability paper shows two theoretical modes at 44·3 and 39·8 units. The populations are closely overlapping, having theoretical ranges of 40–48·5 units and 36–44 units respectively. As a result it was not possible to provide a practical demonstration of any separation of the sexes in the last larval instar.

A few measurements were made of the mandibles of larvae of a related species, *A. nebulosa* (Meigen). These larvae were reared from an egg mass and four instars were demonstrated. The value of r was estimated to be 1·75, i.e. slightly less than that of *A. trifascipennis*. However, because of the small number of *A. nebulosa* which were reared, this estimate can only be regarded as an approximation.

(c) *Procladius choreus* (Meigen)

This species was reared from egg masses and again four larval instars were found. The mandibles of 405 individuals were measured and these measurements conformed to Dyar's rule with a value for r of 1·6 (Table VI).

TABLE VI

	Instars			
	1st	2nd	3rd	4th
Observed mean length of mandible . .	9·10	14·00	22·60	35·87
Estimated mean length of mandible . .	8·80	14·00	22·40	35·84

($r = 1·6$) (1 unit = 0·0038 mm.)

This value of r is similar to the value ($r = 1·63$) calculated by MacDonald (1956) from the third and fourth instars of *P. umbrosus* (Goetgh.).

P. choreus differs from the other species of Chironomidae so far investigated in that the lengths of the mandibles of the last instar larvae show a unimodal distribution. A straight line graph is obtained when the measurements are plotted on arithmetic probability paper. In this species, therefore, it is not apparently possible to distinguish between the sexes in the last larval instar.

(3) *Subfamily Orthocladiinae*

(a) *Cricotopus obtexens* (Walker)

This is the only other species of which a large number of individuals were examined. Measurements were made of the length of the labium in 419

larvae. Four instars were again discovered but it is not certain that their growth conforms to Dyar's rule. The best estimate of r, based on the mean length of the labium in each instar, is 1·65 (Table VII).

TABLE VII

	Instars			
	1st	2nd	3rd	4th
Observed mean length of labium . . .	12·00	19·00	32·92	51·68
Estimated mean length of labium . . .	11·80	19·40	32·00	52·80

($r = 1·65$) (1 unit = 0·0038 mm.)

There is, however, a greater size difference between the second and the third instar larvae than is expected from the theoretical value of r (*cf.* Table VII). This rather poor correspondence between the observed and the theoretical means is interesting, since it was in a species of this same genus that Berg (1950) found Dyar's rule to be inapplicable. A few measurements have been made of the related species *C. sylvestris* (Fabr.). A similar value of r can be applied to the labia of larvae of this species, but again there appears to be an unusually large size gap between the second and third instars. However, the number of *C. sylvestris* larvae which were measured was too small for any definite conclusion to be made.

The measurements made on the last instar larvae of *C. obtexens* are similar to those of *Procladius choreus* in that they have a unimodal frequency distribution. The sexes cannot apparently be distinguished in the fourth larval stage of this species. As in the case of *Prodiamesa olivacea*, the third instar larvae of *C. obtexens* also show a unimodal distribution.

(b) *Corynoneura scutellata* Winnertz

Dyar's rule was found to be applicable to this species of orthocladiine. The four instars were reared from eggs and the labial lengths of 59 individuals measured. Larvae of this species are very small and their growth rate r, was estimated to have the very low value of 1·45 (Table VIII). The fourth instar apparently consists of a single population.

TABLE VIII

	Instars			
	1st	2nd	3rd	4th
Observed mean length of labium . . .	13·40	19·30	27·77	40·93
Estimated mean length of labium . . .	13·40	19·40	28·10	40·70

($r = 1·45$) (1 unit = 0·0038 mm.)

SUMMARY

1. This study of the larval stages of Chironomidae shows that four instars occur in each of the subfamilies which are found in fresh water, thus confirming the suggestion of Thienemann (1954).

2. The increments of growth at each moult have been examined by measuring various structures within the head capsules of each larval instar.

3. In general the growth of the larvae conforms to Dyar's rule but there is a rather poor correspondence between observed and estimated sizes in species of the orthocladiine genus *Cricotopus*.

4. The three species with relatively large full-grown larvae, *Prodiamesa olivacea* (Meigen), *Clinotanypus nervosus* (Meigen) and *Anatopynia trifascipennis* (Zett.) have the highest rates of growth. In these species the last instar measurements show a bimodal frequency distribution which is due to the differentiation of the sexes at this stage.

5. The sexes of the last instar larvae of *Prodiamesa olivacea* and *Clinotanypus nervosus* were subsequently fairly readily distinguishable. The sex ratio of these species was approximately 1 : 1.

6. The antennae of *C. nervosus* provided a good illustration of allometric growth in larval Chironomidae.

7. The species with smaller full-grown larvae, *Procladius choreus* (Meigen), *Cricotopus obtexens* (Walk.), *C. sylvestris* (Fabr.) and *Corynoneura scutellata* Winn. showed relatively low rates of growth. In these species the measurements made on the last larval instar followed a normal frequency distribution. No distinction between the sexes of these larvae was observed.

8. A method of determining the sex of chironomids in the pupal stage has been noted.

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OVIPOSITION BY *MANSONIOIDES* MOSQUITOES IN THE GAMBIA, WEST AFRICA

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The classical breeding places of *Mansonioides* are areas of stagnant water, covered by the floating water lettuce, *Pistia stratiotes* L. (Ingram and Macfie, 1917 ; Iyengar, 1938). The females lay their eggs in compact masses on the floating leaves (fig. 1). Removal of the *Pistia* has been recommended as a method of controlling *Mansonioides* in India (Sweet and Pillai, 1937 ; Iyengar, 1938), and destruction of the plant by herbicides has been recommended as a more economic method of control in Ceylon (Dassanayake and Chow, 1954).

Both Bonne-Wepster and Brug (1939), and Carter (1950) have given lists of other plants on which the egg masses of *Mansonioides* have been found ; Carter recorded 24 species of plant, of which 11 were grasses. Most of these records refer to one species, *M. uniformis* Theob., and both authors found *M. annulifera* Theob., in Batavia and Ceylon, associated only with *Pistia*. Horsfall (1955) has suggested that *M. uniformis* differs from other species of *Mansonioides* in not being restricted to *Pistia stratiotes*, but Galliard (1939), in the northern part of Indo-China, found that, although *Pistia* was present, both *M. annulifera* and *M. indiana* Edw. preferred to oviposit on the floating leaves of a water fern, *Salvinia*, growing amongst water hyacinth, *Eichornia*.

Relatively little has been recorded from Africa about plants used for oviposition as alternatives to *Pistia*. Schwetz (1930) and Hopkins (1952) record the larvae of *M. africanus* Theo. and *M. uniformis* from the roots of grasses and other plants, but Schwetz, in the Congo, could find the egg masses only on *Pistia*. In parts of Zululand, where *Pistia* was absent, Ingram and De Meillon (1927) discovered the egg masses on floating leaves of *Ludwigia* and *Lemna*, and *Lemna* has been used for rearing *M. africanus* (Connal, 1928).

In the Gambia adult *Mansonioides* have been captured near the coast, and inland (Findlay and Davey, 1936 ; Bertram, McGregor and McFadzean, 1958). Descriptions of the Gambia have been given by McGregor and Smith (1952), Smithers (1956) and Bertram *et al.* (1958). The dry season is severe and lasts from November to June, most of the rains falling in the months of August and September. The annual rainfall is about 40 inches. In the dry season most freshwater areas, other than the main rivers and their tributaries (bolons), dry up. During the work reported here three areas in the Gambia were visited : the country around the mouth of the River Gambia near Fajara ; the tidal part of the river, about 40 miles inland, around Keneba ; and the freshwater part of the river, about 160 miles inland, around Bansang. Most of the observations recorded here were made at Keneba, although all suitable freshwater sites here had dried up during the previous dry season. However, conditions during the rainy season appeared to be typical of much of the Gambia.

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Plants Selected for Oviposition

Pistia is uncommon in the Gambia and was found, during the present survey, only in a small pool near the coast at the village of Bakau ; it has, however, also been reported as growing upriver at Bansang (Bertram *et al.*, 1958). *M. africanus* was reared from eggs found on the leaves of *Pistia* at Bakau, and Duke reported *Mansonioides* larvae on *Pistia* growing at Bansang (Bertram *et al.*, 1958). When *Pistia* is absent the plants selected for oviposition were found to be those with floating leaves, growing in the freshwater pools and, as weeds, in the rice fields (*see* fig. 2). It became obvious that some of these floating leaves were preferred for oviposition ; therefore, in order to determine the factors influencing oviposition in *Mansonioides*, two localities at Keneba

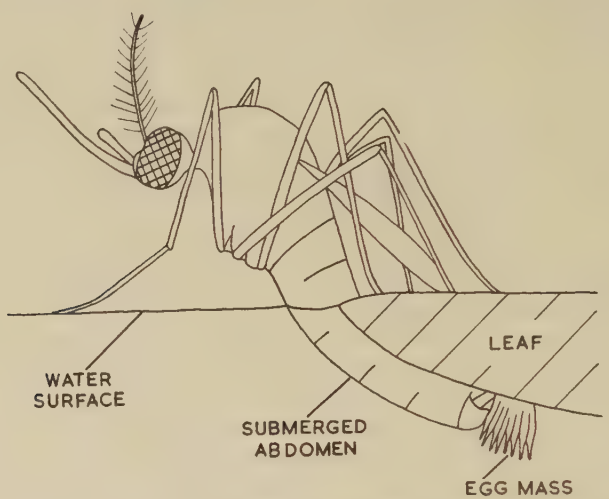

Fig. 1.—Position adopted by female *Mansonioides* when ovipositing beneath floating leaves (drawn from photograph).

were studied in some detail. The first of these was a small pool, pH 6·6–6·7, about 4·5 metres in diameter, containing the water lilies *Nymphaea micrantha* Guill. and Perr. and *N. lotus* L., and surrounded by the grasses *Oryza*, *Echinochloa pyramidalis* (Lam.) Hitch. and Chase, and *Leersia hexandra* Swartz, growing in the water at the edge of the pool. Both *M. africanus* and *M. uniformis* were found, as larvae and pupae, attached to the roots of the three species of grass, although *M. africanus* was the commoner (85 per cent. of a total of 135 larvae and pupae collected). In 1957 the first rains flooded the pool on 17th June and mature fourth instar *Mansonioides* larvae were found in the pond, attached to the exposed roots of the grasses, on 14th July. Gravid females were therefore almost certainly present in the vicinity of the pool during the first week of the rainy season. The pool lay at the edge of a belt of rice fields bordering on a brackish bolon, in which were growing a few shrubs of *Rhizophora*, which defined the outer margin of a belt of mangrove swamp.

The second locality investigated in detail was about half a mile from the pool, and was an unweeded rice field, pH 6·8–7·0, which became flooded between

July and August. *Nymphaea micrantha* was common, and other genera with floating leaves, *Marsilea* and *Heteranthera*, were present, growing amongst the grasses *Oryza* and *Echinochloa*, and other plants. Only larvae of *M. africanus* were found here, attached to the roots of the grasses.

These two areas were visited during August and September at approximately weekly intervals. In addition a smaller area of the grasses fringing the pool, about 1 square metre in size, called here the " experimental area ", was examined nearly every day for two weeks. Towards the end of the study a second unweeded rice field, pH 6·2–6·6, adjacent to the pool and flooded

Fig. 2.—Egg masses of *Mansonioides* on the leaves of various plants: (A) *Nymphaea lotus*; (B) *N. micrantha*; (C) *Marsilea*; (D) *Heteranthera*. (Scale = 5 cm. Size of egg masses exaggerated.)

during August, containing *Oryza* and *N. micrantha*, was brought under observation. Both *M. africanus* and *M. uniformis* were found on the roots of *Oryza*.

Distribution of Egg Masses on *Nymphaea micrantha*

The commonest plant with floating leaves found in all localities was the small water lily, *N. micrantha*, and more egg masses were found on the leaves of this plant than on any other. Leaves floating in open water, such as those in the centre of the pool, were obviously avoided by ovipositing females, and no egg masses were found on leaves which were not floating within 15 cm. of standing emergent vegetation. In contrast around the edges of the pool where the leaves were floating next to, or surrounded by, the grasses fringing the pool, and in the rice fields, where the leaves were floating in small clear areas of water about 30 cm. square and surrounded by grasses and other plants, 35–40 per cent. of the leaves present were used by ovipositing females (Table I).

In the " experimental area " of the pool, which was chosen because this part was obviously favoured for oviposition, two-thirds of the available leaves were used by the females.

TABLE I.—*Comparison of the numbers of egg masses of* Mansonioides *laid on* Nymphaea micrantha *in different breeding places at Keneba*

	Edge of pool	Experimental area of pool	First unweeded ricefield	Second unweeded ricefield
Percentage of leaves with eggs	39·5	62·0	38·6	35·0
Mean number of egg masses per leaf and standard error	1·02 ±0·12	2·22 ±0·44	0·84 ±0·12	0·51 ±0·11
Variance of mean	3·61	9·73	1·90	0·64
Probability that egg masses are distributed at random between leaves*	<0·01	<0·01	<0·01	<0·5 >0·05
Total leaves examined (and number of counts)	258 (3)	50 (3)	127 (1)	57 (1)

* Estimated by comparison of the known distribution of egg masses on leaves with the expected Poisson distribution if the egg masses were distributed at random (using χ^2 test).

There was no apparent difference in the attractiveness, as measured by the average number of egg masses laid per leaf, between the leaves floating in small areas of water in the first rice field, and those floating around the larger water area of the pool. There was evidence in both localities of selection of certain leaves for oviposition (Table I). In the experimental area of the pool, where two-thirds of the leaves carried egg masses, again more leaves than were expected carried no eggs, despite their close proximity in this small area. In the second unweeded rice field, however, there was no evidence of selection of certain leaves for oviposition but, as the floating leaves here were all young leaves, they had probably been exposed at the surface for too short a time for any selection to be obvious. The distribution of egg masses on the leaves of *N. micrantha* showed that the ovipositing females of *Mansonioides* laid their eggs only on leaves floating amongst or near, standing vegetation, and that, of these leaves, some were better situated than others for oviposition.

Effect of Leaf Size on Oviposition

The leaves of *N. micrantha* vary in size and it was possible that their attractiveness for oviposition was associated with size. The egg masses of *Mansonioides* are usually laid at the edges of floating leaves (fig. 1), and the larger leaves would be expected to carry proportionately more egg masses. The relationship between the number of egg masses laid and the size of leaf, recorded at the pool, is shown in figure 3. If the actual distribution of egg masses on the leaves of different size (*see* fig. 3) is compared with the expected distribution, from the average number of egg masses per leaf, the difference between the two distributions is significant ($p < 0{\cdot}01$, $\chi^2 = 19{\cdot}8$, number of size groups = 6), and suggests that the very small and very large leaves are less suitable for oviposition than are those of medium-size.

The reason for the unattractiveness of the larger leaves for oviposition may be related to the behaviour of the female mosquito before oviposition. If a gravid female is placed on a surface of leaves floating on water, the first reaction

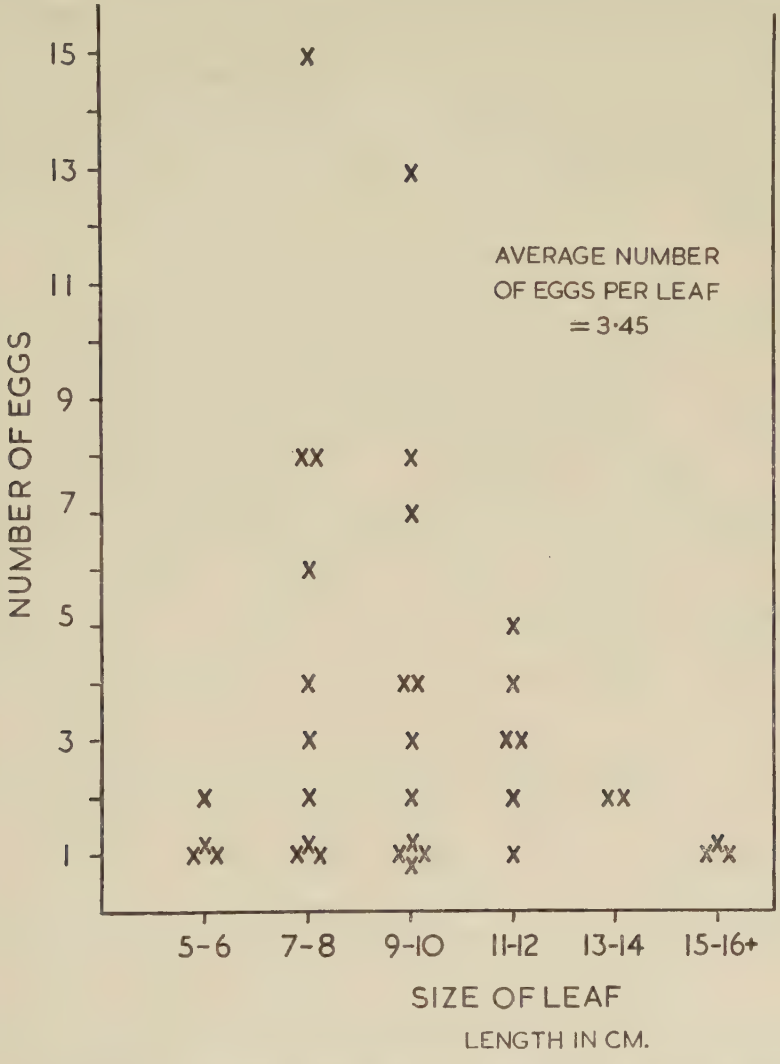

FIG. 3.—Distribution of egg masses of *Mansonioides* on leaves of *Nymphaea micrantha* in relation to size of leaf.

is to walk about dipping her proboscis and apparently testing the water/leaf surface. Once a small water area has been found, the female arches forwards her abdomen, beneath her head and thorax, and attempts to push the abdomen into the place previously located by the proboscis, and then backwards beneath the leaf on which she stands. Oviposition then follows (*see* fig. 1). On a

smaller leaf the searching female would come relatively quickly to a place suitable for oviposition at the edge of a leaf. On a larger leaf, however, the area to be covered is greater and, if it is larger than the area normally searched, the female may fly away before discovering a place suitable for oviposition. This hypothesis is supported by the pattern of oviposition on the very large leaves of *Nymphaea lotus*, which may be 16–30 cm. in diameter. These leaves were rarely used for oviposition and an intact leaf appeared to be too large for the females to find the edge readily. But when the surface of the leaf was fenestrated (*see* fig. 2), several egg masses were then laid through the fenestrations. The smallest leaves are the youngest and have been exposed to ovipositing females for only a short time. Consequently fewer egg masses may be expected.

Oviposition on Leaves in a Small Area

The difference in size of leaves does not explain the aggregation on certain leaves found in the experimental area of the pool, where the leaves examined were of almost equal size. Again, in the first rice field, where the leaves varied from 4 to 10 cm. in length, there was no evidence of leaf size influencing the distribution of egg masses. The expected and the experimental distributions of eggs on leaves of different sizes here did not differ significantly ($p > 0{\cdot}3$, $\chi^2 = 3{\cdot}2$, number of size groups $= 4$). The experimental area consisted of four small pools, each about 30 cm. square, separated from one another by standing rice plants (*Oryza*), and lying within the belt of *Oryza* fringing the main pool. In two consecutive experiments, between 22nd August and 4th September, the pools were first cleared of floating leaves, and about 20 equal-sized leaves of *N. micrantha* were floated on the surface. These leaves were then examined for eggs nearly every day. During this period, the daytime screen temperatures varied between 17·8° and 26·6° C. (64° and 80° F.), and at night between 17·8° and 24·4° C. (64° and 76° F.). The relative humidity varied during the day from 51–90 per cent., and at night from 78–90 per cent.

The results from the two experiments were very similar and are shown in figure 4. Oviposition during the experimental period was regular, as measured by the increase in the number of egg masses laid per leaf, and there was no evidence of sudden mass oviposition as suggested in Zanetti (1931), and by Bonne-Wepster and Brug (1939). In both experiments two-thirds of the leaves carried egg masses after the first two days, and oviposition continued on these leaves on subsequent days. The remaining third of the leaves, which were without egg masses on the second day, were mostly ignored for oviposition on subsequent days, despite no obvious change in the rate of oviposition. Probably, slight differences in the position of the leaves relative to the grasses fringing the pools are important in the selection of leaves by ovipositing females.

Oviposition on Plants other than *N. micrantha*

Egg masses of *Mansonioides* were also found on the floating leaves of grasses (*Echinochloa* and *Oryza*), the larger water lily, *N. lotus*, the water fern, *Marsilea*, and on *Heteranthera callifolia* Reichb.

During August *N. micrantha* was well established in the pool but in July, when both species of *Nymphaea* were just beginning to appear on the surface,

egg masses of *Mansonioides* were laid on the floating leaves of grasses (*Echinochloa* and *Oryza*) which were, in fact, the only floating leaves available for oviposition, amongst the belt of grasses fringing the pool. Again, at the end of September, when the water lilies were dying back, egg masses were found commonly on the leaves of *Oryza*, although they were rarely found on *Oryza* during August, when *N. micrantha* was common amongst the grasses. The

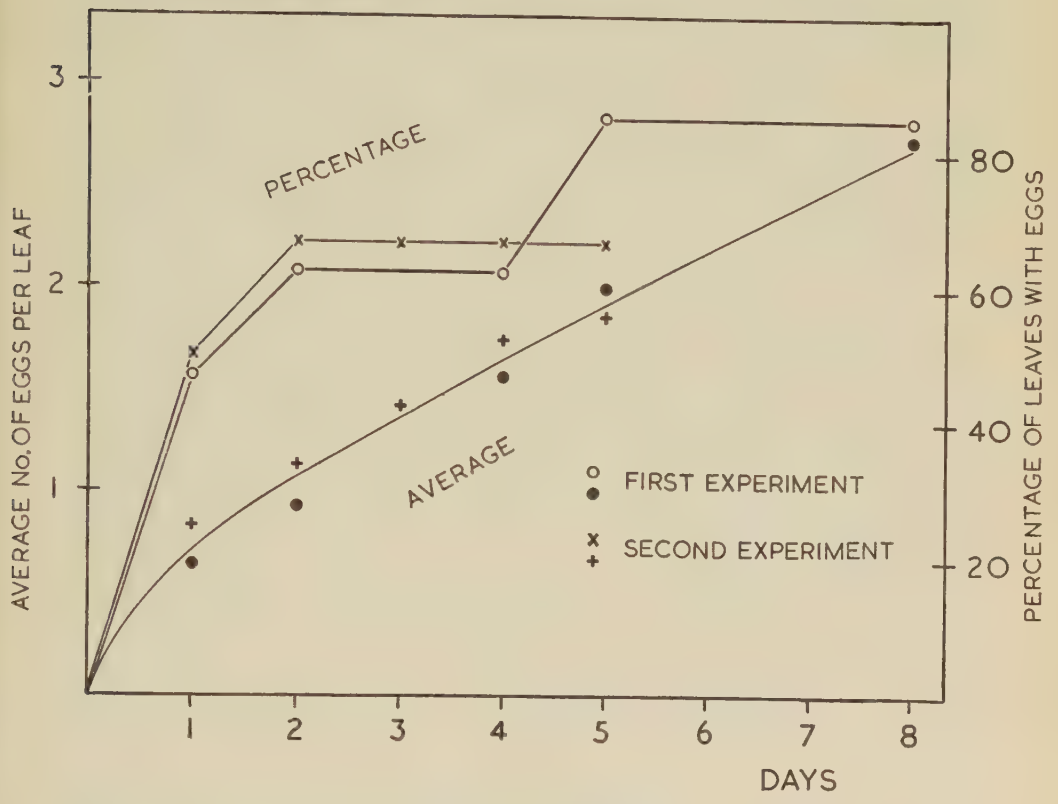

Fig. 4.—Oviposition by *Mansonioides* in the experimental area of the pool, Keneba, showing rate of oviposition (average number of egg masses per leaf) and the percentage of leaves used for oviposition in two experiments over a period of fourteen days.

ovipositing females were therefore able to adapt to different plants as the rainy season progressed.

Oviposition by *Mansonioides* on *Nymphaea lotus* has already been mentioned, and it is suggested that the leaves were normally too large for oviposition. No egg masses were found on intact leaves, nor on fenestrated leaves growing in open water, but they were found on fenestrated leaves growing close to standing vegetation. Only one egg mass, out of 23 on nine leaves, was found at the edge of a leaf; the rest had been laid through fenestrations in the leaves. The other two plants, *Marsilea* sp. and *Heteranthera* sp., were small-leaved and growing mostly in open water in the rice fields. Only a few plants, less than

4 per cent. of those examined, were found with egg masses on the undersides of the leaves, and these few plants were closely surrounded by other vegetation.

Discussion

From the detailed study of the distribution of *Mansonioides* egg masses on floating leaves at Keneba it appears that the females about to oviposit are first attracted to emergent vegetation standing in the water, and not to the floating leaves themselves. This may explain why, in the laboratory, gravid females have difficulty in discovering dishes containing floating leaves placed in their cages. If these females are confined in a small space over the plants, most of them will lay (Wharton, 1957 ; Laurence and Smith, 1958). The behaviour of *Mansonioides* at Keneba is very similar to that of *Anopheles minimus* Theobald in India, where the females select breeding places shaded by standing vegetation (Muirhead-Thomson, 1940, 1951).

The leaves used at Keneba for oviposition were floating flat on the surface of the water and this habit is in contrast to that of *Pistia*, where only the leaves of very young plants float parallel with the surface, and where the tips of the leaves of mature plants may be about 15 cm. above the water surface. It is possible that the more erect leaves of *Pistia* have the same function as the erect leaves of the emergent vegetation when *Pistia* is absent—that of attracting, and possibly providing resting places for female mosquitoes before other stimuli for oviposition begin to operate. Attraction to a breeding place is followed by a search over the leaves at the water surface and, from the rarity of egg masses on intact leaves above 12 cm. in diameter, it is suggested that the search may be limited to an area of less than 200 sq. cm. When an alternating pattern of floating leaf and water surface has been discovered, oviposition follows. Certain leaves are obviously better situated for oviposition than others, even in areas of water as small as 900 sq. cm.

The plants used for oviposition at Keneba, with the exception of the grasses, all had their roots completely submerged in the mud. The roots of *Nymphaea*, *Marsilea* and *Heteranthera* could all be shown to be suitable, in the laboratory, for the attachment and respiration of *Mansonioides*, but only when the mud had been washed from the roots. The larvae and pupae which were collected in the field were attached only to the exposed roots arising from the upper nodes of the stems of the semi-aquatic grasses, which commonly surrounded the floating leaves on which the eggs were laid. The biological advantage of restricting egg laying to floating leaves surrounded by standing vegetation is obvious in view of the transfer from one plant to another during the life history. Galliard (1939) has observed a similar alternation in northern Indo-China, where egg masses were laid on the floating leaves of *Salvinia*, but the larvae were attached to *Eichornia*, a more erect plant floating amongst the *Salvinia*.

The ability of *Mansonioides africanus* and *M. uniformis* to live in areas of Africa where *Pistia* is absent means that the removal of *Pistia* is a doubtful method of controlling these species. In the Keneba district the rice fields were over one mile from the villages, yet *Mansonioides* were captured regularly during the rainy season in the native huts, and biting outside at night in the village. Normal weeding of the rice fields and planting of new rice opens up the vegetation and makes the fields no longer suitable for oviposition. In this

way a number of breeding foci at Keneba were destroyed by normal cultivation. As the development of *Mansonioides* from egg to adult takes at least three weeks at 28° C. (Jayewickreme and Niles, 1952 ; Laurence and Smith, 1958), rotational weeding of rice fields, two to three weeks after flooding, would destroy numbers of *Mansonioides* and, together with clearance of any *Pistia* near the villages, would help to reduce the nuisance of these mosquitoes. Even with such control measures, breeding can still continue in quite small areas of water containing floating leaves surrounded by emergent vegetation.

Summary

1. *Mansonioides africanus* Theobald and *M. uniformis* Theobald in the Gambia are able to breed in the absence of *Pistia*. Egg masses are laid on the floating leaves of several plants, the commonest being *Nymphaea micrantha*.

2. The position of the floating leaf relative to the surrounding vegetation is more important than leaf shape, size or species.

3. No egg masses were found on leaves floating in open water. The female selects breeding places containing emergent vegetation, including grasses, on the roots of which the larvae and pupae are found. The egg masses are not distributed at random between the floating leaves in these breeding places, and some leaves occupy more favourable positions for oviposition than others.

4. Egg masses were rare on leaves more than 12 cm. across. Most of the egg masses found on very large leaves, 16 cm. across or more, were laid through fenestrations in the leaf. This suggests that the female may fly away, without ovipositing, after searching only a limited area of the leaf, if the edge is not reached during the search.

5. The rate of oviposition in one small area did not change markedly over a period of 14 days and there was no evidence of sudden mass oviposition.

6. There was no difference in the numbers of egg masses laid on floating leaves in unweeded rice fields, and on leaves floating amongst the emergent vegetation of small pools. Clearance of rice swamps reduces the breeding area of *Mansonioides*, whereas unweeded rice fields are foci for breeding.

Acknowledgments

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THE PRESERVATION AND MICROSCOPIC PREPARATION OF ANOPHELINE EGGS IN A LACTO-GLYCEROL MEDIUM

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The preservation of Anopheline eggs has up to the present been mainly achieved by keeping the egg-batches on lint or filter paper moistened with dilute aqueous formalin, borax-formol or formol-glycerine (composition given by Leeson, 1937) and by microscopic preparations in the same media, either in hollow slides or (Gabaldon, 1939) in paper cells sealed with du Noyer's compound. Krasikova (1939) found quite a high proportion of eggs preserved in formol to survive in reasonable condition for three years, and eggs in this fluid, sealed into glass capillaries by the method of Perry (*see* Patton and Cragg, 1913 : 417), have apparently been in good condition after nearly 30 years. The latter could not, however, be critically examined under the microscope owing to the cylindrical shape of the tubes.

In addition, solid mounts in gum arabic have been used by Sergent (1936) and in euparal and diaphane by Burton (1953, 1954).

Eggs preserved on moist filter paper are, however, fragile, difficult to handle and prone to distortion after a time, while the dark colour of the laid eggs used in the above mounting techniques is a grave disadvantage. It therefore seems that a need exists for a method of preserving eggs in a fluid medium where they can be easily handled by pipette and in which they are rendered transparent and suitable for examination by transmitted light.

Before oviposition, the eggs within the fully gravid female are morphologically perfect but, not having been subjected to the tanning process, they lack the dark pigmentation of the laid egg. D'Abrera (1944) used such unpigmented eggs for studying the texture of the exochorion. They may be treated by any method suitable for fragile arthropod material, provided that the swelling of the contents can be controlled within rather fine limits. Similar problems exist in the field of soil zoology, and a particularly suitable method is the principle developed by Gisin (1947 *et seq.*) for Collembola and other soil microarthropods. In this technique, lactic acid is used as the clearing agent, and its excessive swelling and clearing action is suppressed by the addition of glycerol and formalin. Anopheline eggs proved too fragile for any of the published formulations, but a modification of the last type of medium has proved satisfactory and the technique extremely simple.

Preservation

Fed female Anophelines are maintained in cages or tubes at a suitable humidity for survival, but no free water is provided for egg-laying. The

mosquitoes attain full gravidity but, with rare exceptions, do not lay eggs. In the Gambia, all species examined during the warm season reached this condition on the morning of the third day after feeding, but under cooler conditions, and in other species, the maturation period is likely to be longer. The mosquitos are killed, the tip of the abdomen then torn off and the eggs extruded by gentle pressure into a drop of the preserving medium on a slide. There is no necessity to damage the specimens excessively and they may be preserved for pinning.

The medium used requires relatively little lactic acid in proportion to the glycerol to give adequate clearing. A satisfactory composition consists of lactic acid (1 part), glycerol (8 parts) and a saturated solution of picric acid in glycerol (1 part). Eggs have now been preserved in this medium for almost a year, without visible sign of deterioration. More recently it has been found preferable to reduce the intensity of the stain somewhat and the medium in use at present has only half the above quantity of picric acid, the deficit being made up with more glycerol. It is important that both the glycerol and the lactic acid should be as nearly 100 per cent. as possible, and in humid climates it is desirable to put a drying tube in the stopper of the container, since the fluid is slightly hygroscopic. The picric acid stains the egg and renders its structures easier to see. This medium clears the objects in about ten minutes and they may then be examined, tubed or mounted by any suitable technique.

Storage

The complete egg batch from a given individual should always be preserved separately and this is conveniently done by drawing the drop of medium into an open ended capillary tube approximately 15 × 1 mm. This is easily achieved with a glass pipette, the nozzle of which enters a hole pierced through a rubber bung, the capillary tube having been inserted in the other end of the hole. When required for further examination or for mounting, the same pipette is used to drive the contents from the tube. Such capillaries may be held in slotted cards, also serving as labels, which should be slightly overlapped by the tubes. Owing to the slightly hygroscopic nature of the medium, these unsealed tubes should not be more than half filled and in humid climates it is an advantage to store over Silica gel. (In practice, no deterioration in eggs was observed without this precaution over a period of more than six months.)

Permanent Preparation

Permanent mounts may be made by any standard method for lactic acid media, the most convenient being the use of cavity slides. Commercial cavity slides may be used but they suffer from the disadvantages that the cavity is too deep to permit orientation of the eggs and that they are rather expensive. This may be overcome by preparing for oneself small cavities in ordinary slides for which purpose Gisin (1958) used a spherical, fine-grain corundum grinder ; one of 15 mm. diameter makes a cavity 3·5–4 mm. wide with a depth of 0·2 mm. and this seems most convenient for Anopheline eggs. The cavities are not polished, but owing to the relatively high refractive index of the medium this is unnecessary. Optimum grinding speed was about 6000 r.p.m.

The quantity of mounting fluid added should fill the cavity but not more than to occupy the greater part of the space between cover-glass and slide. To avoid inclusion of air, the cover should be positioned with one edge first and dropped as soon as it comes into contact with the fluid. At this stage the preparation can be handled and stored in all positions, but for permanent storage it is better to seal them. Alternatively a slight excess of fluid may be used and the cover pressed down firmly under several thicknesses of filter paper. The egg is positioned by lateral movements of the coverslip, the slide washed under a running tap, blotted firmly with filter-paper and allowed to dry before sealing.

The simplest sealing substance is soft wax (paraffin and anhydrous lanolin in equal parts) but " Glyceel ", which is widely used for lactic media in nematology, should prove convenient, though it has not yet been experimented with by the authors.

When cavity slides are not available, the " grease-ring " technique, introduced by Gisin (1947) and improved by von Törne (1953) and Gisin (1955), may be used. This is briefly recapitulated below.

A glass pipette fitted with a plunger and having an orifice of about 0·5 mm. is filled with a neutral molten grease (paraffin wax 10 parts (vol.) + white petroleum jelly (vaseline) 12 parts + anhydrous lanoline 10 parts). When solidified, a thread of this mixture is extruded and applied to an ordinary, thoroughly cleaned microscope slide as an incomplete ring smaller in size than the cover slip to be used. This ring is firmly united to the slide by applying the back of the slide to a heat source such as an electric lamp. The specimens, contained in a drop of the mounting fluid, are placed in the cell so formed and a cover-glass placed on the grease ring. By pressing gently on the cover at different points above the grease ring the fluid is brought into contact with the cover-glass, the thickness of the mount is reduced to the appropriate distance and the fluid is brought near to the opening. Finally, by applying a heated spatula to the back of the slide underneath the opening of the cell, the grease at this point is melted and runs across the interface of the fluid, completely enclosing it. It is not necessary to seal these mounts, but if preferred it may be done with the soft wax described above in connection with the cavity slide technique. Full details of this method may be found in the above papers and in Kevan (1955 : 425–428).

Exochorion Preparations

In the taxonomy of Anopheline eggs the ornamentation of the exochorion is of great importance. Good techniques have been described by d'Abrera (1944) and by Gomez and Millares Manana (1948), but eggs preserved in the lactoglycerol medium described above offer probably the most convenient method at present available of examining this feature. In contrast with laid, tanned eggs, the exochorion may be easily dissected from these preserved eggs and is very suitable for examination by transmitted light under the highest powers of the microscope. Fragments of exochorion may be placed in a drop of the medium on an ordinary slide, covered and the cover-glass firmly pressed down with filter paper. The mount is washed under a running tap, allowed to

dry and sealed with wax (or possibly with " Glyceel "). Such mounts have proved very satisfactory for photomicrography.

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AN ACCOUNT OF PARENTAL CARE IN *RHINOCORIS ALBOPILOSUS* SIGNORET (HEMIPTERA-HETEROPTERA: REDUVIIDAE), WITH NOTES ON ITS LIFE HISTORY

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Introduction

Parental care has been reported in eleven species of the Hemiptera-Heteroptera, an order of non-social insects, the species concerned belonging to the following families: Pentatomidae (four species, each in a different genus), Acanthosomidae (two species in the same genus), Phloeidae (one species), Meziridae (one species), Tingidae (two species in the same genus), Emesidae (one species), and Reduviidae (one species). At least one example of parental care occurs in all the major zoogeographical regions. For a summary of the literature the reader is referred to the excellent paper by Hussey (1934); additional observations are reported by Frost and Haber (1944) and Kirkpatrick (1957).

One essential feature of all reported cases is that the insect taking care of the young brood (eggs or nymphs as the case may be) never flies away when disturbed, though in other situations it would take alarm and fly away. In all the families, except the Meziridae and Reduviidae, it is the female that looks after the brood; in the case of the Meziridae it is not known which sex is concerned, though it is thought to be the male; in the Reduviid *Rhinocoris albopilosus* Signoret it is definitely the male.

A similar case of parental care has been reported in the Membracidae (Hemiptera-Homoptera). In this family it is the female that stands guard over her offspring (Imms, 1957: 440).

Bequaert (1912, 1913; and Schouteden, 1912, commenting on Bequaert's observations) on several occasions in the Belgian Congo observed males of *R. albopilosus* standing guard over egg masses. When disturbed, the male raised its head and rostrum in the direction of the danger; when he tried to capture it, it ran away for a short distance but returned to the egg mass as soon as the danger had passed.

Apart from Bequaert's original observations on this species, the present writer has been unable to locate any further observations on this interesting habit, some of the most recent summaries of the biology of the Reduviidae merely repeating Bequaert's report (*e.g.* Miller, 1953; and Villiers, 1948: 20–21). Indeed, Miller has gone so far as to state (p. 550): "One author [referring to Bequaert] . . . has referred to an instance in which a male remained on or close by a mass of ova until eclosion took place, but he does not make it clear whether the period of standing over the ova covered the entire incubation period, which would not be less, presumably, than fifteen days. It appears to me that, in this case, the presence of the male was entirely fortuitous, or more probably, the reason for the male being near the ova was that it was about to devour them."

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The present writer has made observations on *R. albopilosus*, both in the field and in the laboratory, in Uganda : at Serere Experiment Station (in the Eastern Province) from late August to late September, 1957, and at Kawanda (Buganda Province) from the middle of November, 1957, to the middle of April, 1958. As a result, Bequaert's original observations on parental care in this species have largely been confirmed and considerably extended ; information has been obtained on the following points : the feeding behaviour throughout the life-cycle ; the behaviour of the male and female from the moment of copulation ; the continuation by the male of its parental care to include the early life of nymphs and the capture of food for them. During the course of these observations some information on the life history of the Reduviid was obtained, and this is also included here.

In this paper, the habit of guarding eggmasses by either sex in the Heteroptera will be referred to as " brooding."

Notes on the Life History

Habitat

At Kawanda, *R. albopilosus* frequents *Stylosanthes mucronata* Willd. (Leguminosae), a low spreading shrub, 2 feet high, which generally grows in thick mats in open fields. Though the Reduviid probably frequents other plants, this has not been ascertained ; in any case, *Stylosanthes* grows so commonly at Kawanda that it was found convenient to concentrate field studies of *R. albopilosus* on this plant. At Serere, in the single case of brooding noted, the eggmass was laid on the grass, *Panicum maximum* Jacq.

Oviposition

R. albopilosus lays eggs in compact masses, arranged in 4–6 long rows along a plant stem ; the eggs are fixed with their long axes vertical to the plant stem. On *Stylosanthes*, the eggs were normally laid on stems 6–12 inches from the ground ; on *Panicum* they were laid some 4–5 feet from the ground. Eggmasses found in the field were large, sometimes consisting of more than 250 eggs ; as a rule, however, a single female laid about 80 eggs in the laboratory. The eggs in a batch were often so closely packed that their opercula appeared hexagonal.

Females ready to lay have greatly distended abdomens. Laying females were observed on several occasions in the laboratory. The female lowers the apex of her abdomen on to the substratum, remaining immobile for a minute or so. The tip of the abdomen rises gradually, partially revealing an egg stuck on to the substratum ; the movement stops for a moment in the middle, then it is resumed and the abdomen expels the top of the egg suddenly, like a cork from a bottle but without the " pop." One series of records was made of the time it took to lay individual eggs : 5th egg (70 secs.), 6th egg (140 secs.), 7th egg (165 secs.), 8th egg (95 secs.), 13th egg (about 35 mins.) ; subsequent eggs (up to 17th) took much longer.

A female usually lays several batches of eggs before completing oviposition, and the oviposition period may extend over several days, from four to twelve, the interval between laying sessions varying between one and five days. Two batches of eggs may be laid during the same day, but this is unusual.

Laying starts only a few hours, or at most a few days, after mating ; it was most common during mid-morning and early afternoon.

Miller (1953 : 552, 623 ; 1956 : 109) states that in the genus *Rhinocoris* Hahn, the female, after completing oviposition, usually secretes a glutinous substance which she spreads on to the sides of the egg mass, with the exception of the opercula. In the case of *R. albopilosus* this was not observed. The bases of the eggs are stuck on to the plant stem and to each other by a glutinous substance.

Life History

Newly laid eggs appear light brown, but later become much darker. The incubation period is 12–14 days in the laboratory. Hatching, which is accomplished by the nymphs pushing off the opercula, extends over several days in the case of large egg masses and may occupy 7–20 days. It is most common at about 10 a.m. Each emergence takes about 10–15 minutes ; after 5–10 minutes the nymph moves away from the egg-case, which contains the embryonic membranes. At first newly emerged nymphs are yellowish or pale, with black eyes and red patches on the abdomen ; they later become quite dark or black, this blackening process occupying three hours or more.

A batch of 12 nymphs which emerged in the laboratory were bred individually in order to obtain an indication of the length of the life-cycle. Of these, two died during the second and third nymphal instars respectively. The results are presented in Table I. The length of life of the adults was not determined, but those caught in the field have been kept in captivity for as long as two months ; the females appeared to live longer than the males.

TABLE I.—*The life history of* 5 *male and* 5 *female* Rhinocoris albopilosus *Sign. bred individually at room temperature in the laboratory at Kawanda, December* 1957 *to March* 1958

Duration recorded in days

	Male		Female	
Nymphal instar	Mean	Range	Mean	Range
I . .	10·8	10–14	11·6	11–12
II . .	8·6	8–9	10·2	8–16
III . .	14·2	10–18	13·8	7–18
IV . .	10·8	8–13	11·4	7–14
V . .	22·0	18–26	24·4	22–27
Total nymphal stage . .	66·4	56–71	71·4	68–74
Adult : pre-oviposition period .	.	.	12·4	9–20

Feeding Behaviour

In the laboratory, the earlier instars were usually reared on thrips, which were regularly collected from the heads of *Chloris gayana* Kunth., a common grass at Kawanda on which *Haplothrips stofbergi* Faure is abundant. From the fourth instar, the nymphs, and later the adults, were usually fed on

fruit flies (mainly *Drosophila* spp.) bred on bananas ; sometimes, however, the Reduviids were offered a variety of small insects swept from cotton, maize tassels, and *Stylosanthes*, including beetles, bees, leafhoppers and shield bugs, which they readily accepted.

Both fruit flies and thrips were introduced into several breeding cages in order to study the feeding preferences of *R. albopilosus*. In such cages, four first instar nymphs (8 days old) were in one instance seen holding on to a Drosophilid fly and sucking it. Occasionally third instar nymphs were seen feeding on Drosophilid flies, especially in the morning. In these instances, it was thought that the flies that were caught by the young nymphs were exhausted ones, especially as, in almost every case, the feeding took place on the floor of the cage. The younger nymphs appeared to prefer thrips. A change-over of food preferences seemed to occur at the fourth instar, when nymphs readily attacked flies whenever offered. It is interesting to note that cannibalism was most frequent at this stage, the older nymphs feeding on the younger ones ; this happened if only thrips were offered when some of the nymphs had already attained the fourth instar. At the fifth instar, they definitely preferred flies ; thrips were apparently entirely unmolested ; this preference continued into the adult stage.

It is postulated that in the earlier nymphal stages *R. albopilosus* feeds on the thrips and other similarly minute insects occurring on *Stylosanthes*. On *S. mucronata*, at Kawanda, two species of thrips have been collected in numbers : *Haplothrips gowdeyi* (Frankl.) (Phlaeothripidae) and *Frankliniella* sp. (Thripidae), the latter being the more numerous. From the fourth nymphal instar and during adult life the Reduviids probably feed on the various larger insects frequenting *Stylosanthes*.

It was thought by Miller (1953 : 555–556) that in the Reduviidae feeding is not essential in the first nymphal instar, provided the nymphs satisfy their water requirements by imbibing dew, etc. Field and laboratory observations in Uganda showed that, in general, nymphs of *R. albopilosus* did not appear to feed for the first two or three days of their nymphal life, and they remained clustered together on or near the egg mass. But thereafter they dispersed and began hunting for food regularly. In one test, however, when hundreds of thrips were introduced into the breeding cage only four hours after the emergence of the Reduviid nymphs, the latter promptly fed on the thrips.

Parasites

Failure to hatch under laboratory conditions was observed in 11–50 per cent. of the eggs laid in the laboratory and of those collected in the field. Unhatched eggs included infertile ones as well as some in which dead, partially developed embryos were found ; in addition 10–20 per cent. of the eggs collected in the field were also parasitized. Two species of egg-parasites were found at Kawanda on egg masses collected on *Stylosanthes*, both apparently equally common : *Hadronotus antestiae* Dodd and *Hadronotus* sp. nr. *hiberus* Nixon (Proctotrupoidea : Scelionidae). The two species were reared from the same egg mass on one occasion.

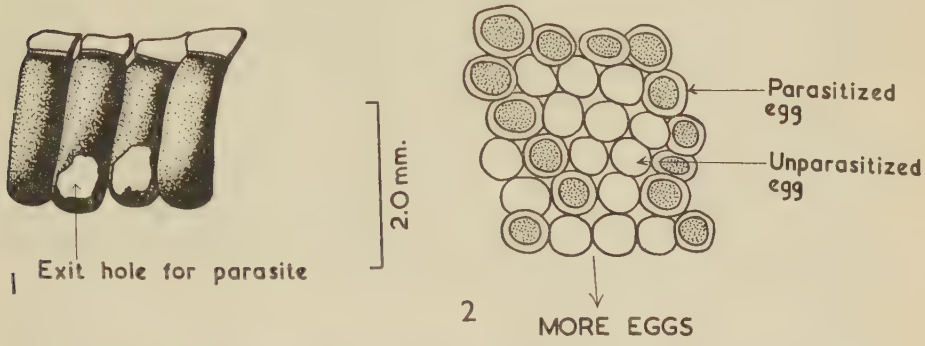
Apparently only one parasite emerges from an egg. When fully grown it is oriented with the head pointing towards the base of the egg, and the body

filling almost the whole egg. It emerges by eating a hole near the base of the egg, the circumference of the hole usually appearing jagged (fig. 1).

Parasitism was more frequent in the larger egg masses, and the parasitized eggs were generally found among the outside rows (fig. 2). The emergence holes of the parasites were usually made on the side external to the egg mass.

Mating

All the laboratory observations concerning mating and parental care were made on adult *R. albopilosus* kept in large cages, 15 inches high and 8 inches in diameter ; branches of *Stylosanthes* were provided for support and laying purposes.



Figs. 1–2.*Rhinocoris albopilosus :* (1) eggs seen from the side, showing exit holes of *Hadronotus* adults ; (2) portion of egg mass as seen from the top, showing the arrangement of parasitized eggs.

After more than a week of adult life, a male generally approaches a female from the rear or from the side and mounts, using the front and middle legs. More often than not, the female resists the male, which may be shaken off several times before he succeeds in getting a firm hold, after which he assumes the following posture : the antennae are swept back ; the tip of the rostrum engages with the " ledge " formed by the anterior margin of the pronotum of the female, or the rostral tip merely holds on to the anterior pronotal lobe ; the front legs grip the sides of the anterior lobe of the female prothorax or the sides of the head ; the middle pair of legs hold on to the thoracic sides immediately above the female middle and hind coxae ; the hind pair hold on to the sides of the abdomen, on the fifth to seventh segments. In this way, the male may " ride " on the female for several hours, the pair constantly on the move, but the female occasionally stopping to preen herself.

While the male is riding on the female, he extrudes the genital segment, the pygophore, and now and again attempts to mate with her. The extruded pygophore is manoeuvred to the left or right of the tip of the female's abdomen and, in a successful attempt, pressed against the genitalia. Once mating commences, the female stops moving about and the pair remain *in copulo* for about 10 minutes. The male then withdraws its pygophore, and the pair once again resume wandering, the male still riding on the female. Mating

usually took place in the early afternoon, though it has been observed from mid-morning to late afternoon.

Females which were successfullly mated were normally those having distended abdomens, presumably containing developing ova ; these appeared less active than other females. During the two or three days following the first mating, the female may mate several times more before depositing her first batch of eggs. During the intervals, the male may disengage himself and leave the female for many hours. It would appear, from laboratory observations, that the same male is involved in subsequent matings ; but whether this in fact is the case in nature needs confirmation.

Parental Care

The male remains riding on the female several hours after completing mating. It has been noted in the laboratory that if the female does not lay any eggs within 3–5 hours after mating, the male generally disengaged himself and left the female. Should the female start ovipositing before disengagement—and sometimes she does so only a few minutes after mating—the male may still disengage himself from the female but he takes up a position at one end of the egg mass ; he does not seem, however, to stimulate the female in any way. Immediately after laying, the female leaves the vicinity of the egg mass, and the male moves nearer or even stands over it.

Behaviour of the " Brooding " Male

The guarding of the egg mass (" brooding ") begins from the moment the female leaves her eggs and the male moves in to stand over them. A brooding male usually stands over the egg mass, with the legs gripping the stem on either side of it, and the body only a short distance above the top of the eggs. Quite frequently, however, the male takes up a position on either side of the egg mass, with the front legs, and often middle ones also, touching or resting on some of the eggs ; sometimes, too, the male merely stands near the egg mass. The antennae occasionally touch or rest on the eggs or hover over them ; in addition, the rostrum occasionally moves over the eggs, touching some of them. A brooding male may change its position many times within a single day, sometimes facing up, sometimes down, the stem.

In the field, if nymphs or adults are disturbed they quickly flee down to the mat of criss-crossing stems of *Stylosanthes*, and the adults may even fly away. Brooding males if disturbed, on the other hand, do not fly away ; when the writer moved within a foot of a brooding male, or probed it with the fore finger, it merely moved to the far side of the stem, and as soon as the writer retreated it returned to its former position. A stem supporting a brooding male has, on several occasions, been removed from the field and carried in the hand or kept in a container for an hour or so ; when the writer reached the laboratory the males were still standing over or near their egg masses.

At Serere, a brooding male was kept under observation from 26th August to 5th September (egg hatching commenced in the middle of this period). Frequent visits were made each day from 7.45 a.m. to 10 p.m. Not at any time during this period was the male found away from the egg mass. There were

frequent high winds and it rained on seven occasions, but the male never left its brood to take shelter.

From the many observations made it appears almost certain that the male never leaves the egg mass to hunt for prey. In several instances flies were introduced into cages containing brooding males. The male did not leave its brood, but if a fly came near, it caught it and fed on it while continuing to brood on the egg mass. If thrips were offered instead, the male seemed uninterested, even when they crawled on to his body, including his antennae. No instances were noticed of the male feeding on his egg mass or on the emerged nymphs.

During the first two days of brooding, and also towards the end of the brooding period, the male seemed more restless. When offered flies in numbers, he sometimes left the egg mass for a few minutes to catch a fly ; but once he had fed on one, he appeared to lose further interest and went on brooding ; on subsequent days he only attacked flies coming to the egg mass.

Behaviour of the Brooding Male and the Newly Emerged Nymphs

It has been stated by Miller (1953 : 555) that nymphs emerging from eggs normally laid in egg masses by Reduviids generally remain clustered together for several days until the first moult is accomplished. The present writer's observations on *R. albopilosus* show otherwise. For the first two or three days the nymphs do cluster together on the empty egg-cases or near the egg mass. On several occasions, however, a batch of newly emerged nymphs have been seen dispersing from the egg mass on the same day that they emerged ; in one instance they did so only 20–30 minutes after emergence. In any case, the nymphs were always scattered by about the third day, which is at least a week before the first moult.

While the eggs are hatching from the egg mass, the brooding male stays on the opposite end to the one from which hatching is proceeding ; it may even move to a nearby branch, returning to its egg mass afterwards. The male does not appear to take care of the nymphs in any way, though they have often been seen climbing onto the male. From 2–20 days from the start of hatching, but usually within a week or so, the brooding male leaves the egg mass entirely. This generally happens before all the healthy eggs have hatched ; in fact most nymphs usually emerge after the departure of the male.

Behaviour of the Laying Female

A female leaves her first batch of eggs as soon as she has deposited it. For the next 4–12 days, the oviposition period, the female lays more batches of eggs. In the laboratory, she invariably added these subsequent batches to the first one. The female comes to the egg mass, turns round until the tip of her abdomen is near the last egg of the outside row, and starts laying eggs below the latter—in line with the other eggs. The large masses of eggs usually found in the field are probably built in this way, and it is extremely difficult to detect any conspicuous break in the sequence to correspond with the separate batches, though often the outside rows are rather irregular in outline.

The first batch of eggs is usually laid with the female's head pointing downwards, which is the normal laying attitude, but sometimes the additional

batches are laid with the head pointing upwards. As in the first case, the female leaves the egg mass as soon as she completes ovipositing.

While laying the female remains immobile, almost rigid, her abdomen being the only moving part of the body, and she does not easily take alarm when disturbed. During the intervals of laying batches of eggs, the female feeds actively.

During the oviposition period, and while the male is still brooding on the egg mass, the female goes to it quite regularly and copulates with the brooding male ; she then leaves the egg mass usually without laying any eggs. As in the first mating, the male climbs on to the back of the female, but in this instance the pair remains standing over the egg mass or moving sluggishly nearby. The riding generally takes much less than an hour before the male succeeds in mating. When this is completed, the male returns to the egg mass. On one occasion, a brooding male tried to mate with a female which had just completed laying a batch of eggs, but the female turned quickly away.

The fact that the eggs are of different ages is undoubtedly the reason why eclosion stretches over several days.

Experiments with Marked Reduviids

A number of experiments were set up with marked unmated adults of both sexes of *R. albopilosus* reared in the laboratory to elucidate some aspects of parental care that had not been covered. The distinguishing marks were made by using white permanent ink. The bugs were placed in large cages, supplied with *Stylosanthes* stems for support and laying, and fed on fruit flies.

Experiment I.—A female was introduced into a cage containing an egg mass, in which most of the eggs had already hatched. The former male and female had been removed. Four days later a male was introduced into the cage and within the same day started brooding on the old egg mass. In the late afternoon of the fourth day after the introduction of the male, the female laid a batch of eggs, about 20 cm. away from the old egg mass, on another stem. Next day the male left the old egg mass and started brooding on the second one.

Experiment II.—Two males (A, B) and two females (P, Q) were placed in another cage. Five days later, male A and female P mated ; the latter laid her first batch of eggs the following day. Another five days later, the second female, Q, laid her first batch of eggs, adding them to those of female P. During subsequent days, the two females added their eggs to the single egg mass ; and both of them were observed mating with the brooding male. At first, male A (which had mated with female P) was in possession of the egg mass ; but an hour afterwards the second male, B, took possession. For the next two days the two males vied with each other for the possession of the egg mass, first one and then the other standing over it ; sometimes male B went away to hunt for prey. The males took up positions on opposite ends of the egg mass ; there was no actual fighting, and what factors decided which male took possession were not determined. At the end of the second day, male A finally took possession ; the second male went away and did not return to the egg mass during the further month that the experiment lasted, nor was it seen to attempt mating with the two females.

Experiment III.—One male (C) and two females (R, S) were caged together.

A week later, female R, which had been mated and ridden by the male for the previous two hours, started laying eggs, the male still riding on her. The laying lasted from 2.05–3.02 p.m. Meanwhile, the second female, S, started laying eggs at 2.45 p.m., less than 1 cm. away from the first egg mass. As soon as female R completed laying (she laid 23 eggs), she moved away and left the male guarding her eggs ; female S was still in laying position, and remained there till 3.20 p.m., by which time she had laid only 3 eggs. The brooding male took charge of the two egg masses by standing between them, sometimes with the front legs on the first egg mass and the hind legs touching the second.

Two days later, female S was seen in the laying attitude near the first egg mass ; after staying thus for 5–10 minutes without laying she went to the second (her own) egg mass. A few minutes later female R moved her out of position and went on to add more eggs to the first egg mass for the next quarter of an hour. As soon as female R left the egg mass, the second female returned to the latter and added 19 eggs to it ; as a result the two formerly separate egg masses ran into each other. During the next four days, the two females returned to the combined egg mass to mate with the brooding male and to lay more eggs.

Experiment IV.—Two males (D, E) and one female (T) were caged together. Three days later, the female started laying, with male D which had mated with her the previous day riding on her again. Male E, meanwhile, was on the far side of the cage. I removed male D from the back of the laying female to another branch of *Stylosanthes*. An hour later, after catching and feeding on a fly, he returned to the egg mass and climbed back on to the still laying female. The next day, at about 3 p.m., the second male, E, was seen approaching the egg mass and taking up a position about 2 cm. away from it. By 6.50 p.m. he had taken over the brooding ; male D went to the opposite side of the cage and was not seen near the egg mass again.

Although the above experiments are only of a preliminary nature, we may draw the following conclusions from them : within a restricted area, and with a small adult population, laying females add their eggs to a single egg mass ; if there is more than one male, the two compete for the possession of the egg mass until only one remains brooding on it ; a laying female does not add her eggs to an old egg mass whose eggs have already hatched ; instead she starts a new cluster.

Discussion

In considering the significance of parental care observed in various Heteroptera, early theorists usually suggested that the habit may have arisen in order to protect the young brood from predation by the male of the same species. This suggestion has been attacked by many subsequent authors, and it cannot be maintained in the case of *R. albopilosus*, where it is the male that does the brooding. A more attractive theory, and one which has been advanced by Dodd (1904), Bequaert (1912), Ayyar (1920), Ballard and Holdaway (1926 : 333), Hussey (1934), and Kirkpatrick (1957 : 257–258, figs. 138, 139), is that this habit results in the protection of the ova—to a considerable extent—from egg-parasites.

Bequaert reported that he had seen a female parasite of the family Pteromalidae approaching an egg mass of *R. albopilosus* several times, but each time

the brooding bug turned towards the parasite and succeeded in preventing it from ovipositing in the Reduviid egg mass. The second direct observations were reported by Ballard and Holdaway in the case of *Tectocoris diophthalmus* (Thunberg) (= *T. lineola* Fabr.): "A [brooding] female was seen moving this way and that and agitating her body while three Chalcid parasites were trying to dodge her and have time to lay their eggs. Eggs thus seem to be protected from predacious insects." The other four authors mentioned in the last paragraph reported only circumstantial evidence. Dodd stated that brooded eggs in *T. diophthalmus* were unparasitized. In the case of *Cantao ocellatus* Thunberg, Ayyar reported that the brooding female does not cover the whole egg mass; the eggs round the edge were parasitized by *Telenomus indi* Girault. Hussey noted that 15 per cent. of the eggs of *Pachycoris torridus* (Scopoli) do not develop, and appear to be parasitized; these eggs occurred only in the part of the egg mass not normally covered by the body of the brooding female. Kirkpatrick recently reported a similar case in *Mecistorhinus tripterus* (Fabr.).

These observations, coupled with those made by the present writer in the case of *R. albopilosus*, suggest that the significance of the brooding habit may be that it results in the majority of eggs laid escaping parasitism. In this connection, it is interesting to note that the brooding habit has only evolved in those species laying their eggs in large clusters and in apparently exposed situations. In cases in which parental care is extended to include the nymphal instars, as in *Meadorus lateralis* (Say) reported by Frost and Haber (1944), it would appear that this care also affords some protection both from parasites and predators; but no information is available on this point. One of the problems that remains unexplained is why the habit is so sporadic in the Heteroptera.

Bequaert's interesting supposition (Bequaert, 1912; Villiers, 1948) that in *R. albopilosus* the male captures prey for the young nymphs has not been supported by observations made in Uganda.

Acknowledgments

The author wishes to record his thanks to the following: Mr. J. Bowden, Senior Entomologist, Uganda Department of Agriculture, for his interest and suggestions during the course of this work; Mr. J. C. Davies for critically reading the original manuscript; Messrs. J. Y. Omiat and S. Kiggundu for taking charge of the breeding work; Miss M. E. Griffiths, formerly of Kawanda, for plant identifications; Messrs. C. F. W. Muesebeck (U.S. National Museum) and G. E. J. Nixon (Commonwealth Institute of Entomology, London) for identification of *Hadronotus* spp.; Dr. H. Priesner, of Cairo, for identification of thrips; Dr. R. F. Hussey (University of Florida, U.S.A.) for generously providing a copy of his paper; and to my wife for helping me with observations at Serere.

Summary

1. Parental care and the life history of *Rhinocoris albopilosus* Signoret (Reduviidae) were studied in Uganda, both in the laboratory and in the field.

2. After mating, the male continues to ride on the back of the female until the latter lays her eggs. When laying is completed, the female leaves the

vicinity, but the male remains to guard the egg mass ("brooding") until a few days after hatching has started.

3. The oviposition period lasts from 4–12 days, during which the female lays several batches of eggs. All the batches are added to the first egg mass. Females in the neighbourhood may also add their eggs to this egg mass. During oviposition the laying female repeatedly mates with the male.

4. The young nymphs readily accepted thrips when offered for food; from the fourth instar, however, they showed a definite preference for larger insects like fruit flies and various plant bugs, bees, and beetles. Brooding males did not go in search of food, though they often caught flies which came near their brooding places.

5. The duration of nymphal life was about 8–10½ weeks in the laboratory, the females taking about a week longer than the males.

6. Two egg-parasites were bred from egg masses laid on stems of *Stylosanthes mucronata* Willd. (Leguminosae) at Kawanda, Uganda, namely *Hadronotus antestiae* Dodd and *Hadronotus* sp. nr. *hiberus* Nixon (Scelionidae). It is suggested that the brooding habit helps in keeping away egg-parasites.

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THE ANATOMY OF THE CENTRAL NERVOUS SYSTEM AND RETROCEREBRAL ENDOCRINE ORGANS OF THE LARVAE OF *LUCILIA CAESAR* L. AND CERTAIN OTHER DIPTERA CYCLORRHAPHA

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[Communicated by Dr. A. R. Hill]

I. Introduction

Weismann (1864) was the first to describe the anatomy and development of a Cyclorrhaphan larva, *Calliphora* (*Musca*) *vomitoria* L. This was followed by the less satisfactory study of the larva of *C. erythrocephala* Mg. by Lowne (1890–92). An excellent account of the anatomy of the mature larva of *Musca domestica* L. was included in a comprehensive work on the house fly by Hewitt (1910). Others have made studies of the morphology and development of the head of these larvae without contributing to knowledge of the central nervous system, but Ludwig (1949), in describing the anatomy of the anterior part of the larva of *C. erythrocephala*, provided new information on the nerves from the cephalic and suboesophageal ganglia. These works formed the background of information for this anatomical study.

II. Material and Techniques

Mature third instar larvae, taken at stages between the cessation of feeding and puparium formation, were used. They were dissected in a saline solution prepared to the formula given by Williams (1946).

For supra-vital staining of the nerves a 1 : 1000 solution of methylene blue in the saline defined above was used, following the procedure recommended by Ludwig (1949). Serial sections were prepared from material fixed in Bouin's fluid and embedded in Steedman's ester wax. Sections were cut at 6 or 8 μ and stained in accordance with a standard haemalum-eosin procedure.

III. The Central Nervous System in the Larva of *L. caesar*

Hewitt observed that in *Musca* " the central nervous system of the larva has attained what would appear to be the limit of ganglionic concentration and fusion ", and Ludwig found that in *C. erythrocephala* " the central nervous system is a very compact mass of tissue, showing no external signs of segmentation. All the ganglia of the head, thorax and abdominal segments are fused into a single mass ". These descriptions could also be applied to *Lucilia* spp.

The brain of the generalised insect is composed of three pairs of cephalic ganglia, those of the proto-, deuto- and tritocerebrum. In the larva of *L. caesar*, as in all Cyclorrhaphan larvae anatomically investigated so far, the component ganglia of each half of the brain are fused to form the two cerebral hemispheres

(*CH*).[1] These are united, dorsal to the foramen traversed by the oesophagus, by the pars intercerebralis, and ventrally each is fused directly to the sub-oesophageal ganglion which forms part of the single ventral ganglionic mass. The membranous frontal sac (*FS*) containing the imaginal discs of the eyes (*IDE*) and antennae (*IDA*) is bifurcate posterior to the bucco-pharyngeal

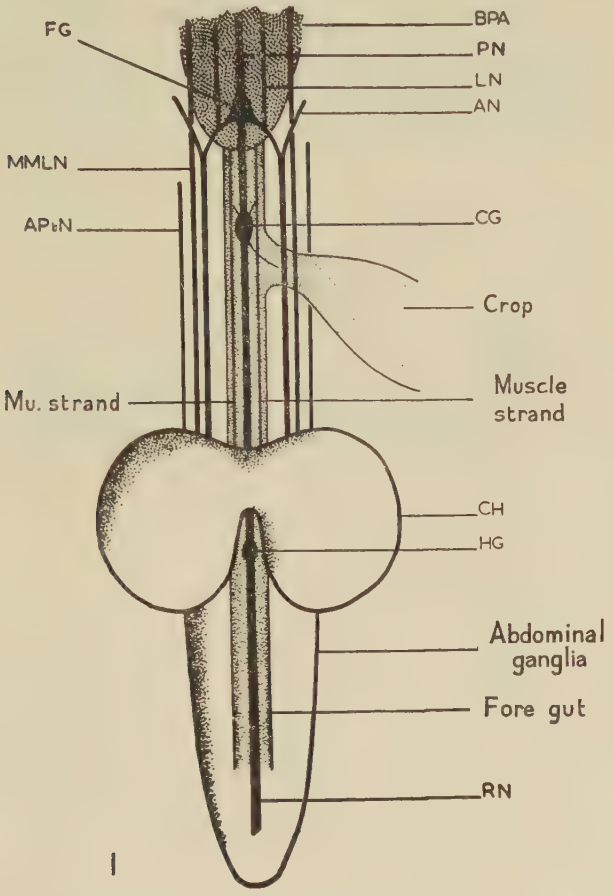


Fig. 1.—Dorsal aspect of central nervous system of larva of *L. caesar*. (For explanation of lettering see text.)

apparatus. Posteriorly each branch of the sac unites to the ventrolateral surface of its corresponding hemisphere by the so-called optic stalk (*OS*). The eye discs fit closely to the anterior surfaces of the hemispheres and within each branch of the sac the antennal disc lies in front of the eye disc. The dorsal aorta (*DAo*) passes as a closed tube over the larval brain but just in front of the pars intercerebralis it opens ventrally, the margins of this opening being fused laterally to the two branches of the frontal sac and posteriorly to the

[1] The letters in brackets are the abbreviations used on figures 1–4.

surface of the brain. In a fresh dissection of a living larva haemocytes carried forward in the blood flowing along the aorta can be seen falling down from this opening between the eye discs into the body cavity. Other connections between the aorta and brain are described later.

IV. Nerves from the Brain and Ventral Ganglia in *L. caesar*

From the ventro-anterior surface of each hemisphere issues a thick nerve which passes forward (*A + LFN*). Its first branch (*AN*) innervates the larval antennal organ, its second branch (*LN*) the labral sense organ, and the nerve

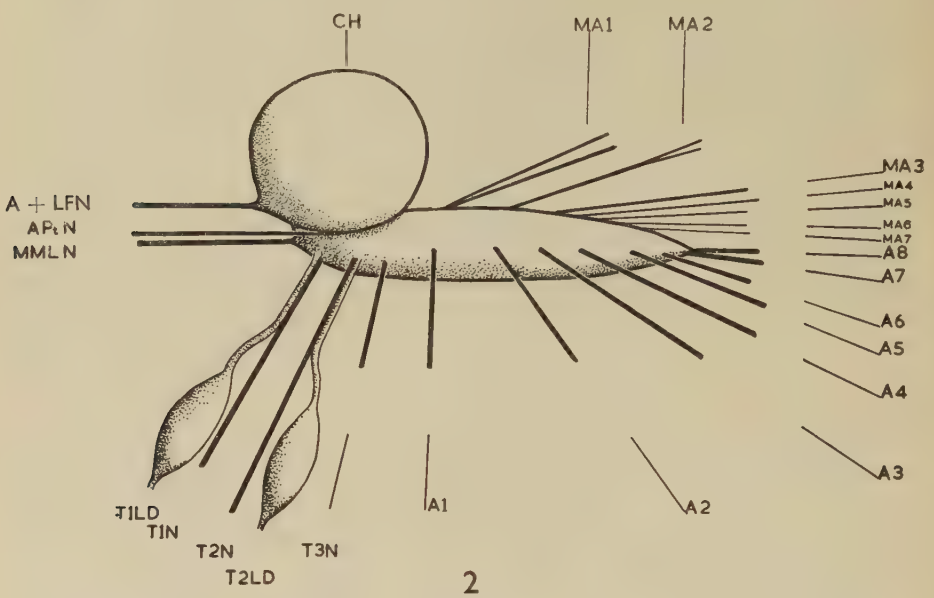


Fig. 2.—Lateral aspect of central nervous system of larva of *L. caesar*. (*A + LFN*, antennal-labro-frontal nerve; for other lettering see text).

terminates in the frontal ganglion (*FG*), which lies on the surface of the pharynx concealed by the muscles of the bucco-pharyngeal apparatus (*BPA*). This nerve can be considered as a fusion of the antennal and labrofrontal nerves. Just below it there emerges from the ventral ganglionic mass, on each side, a nerve which sends branches to the labial sense organ, to the mandibular muscles and to the maxillary palp. It can, therefore, be identified as the mandibular-maxillary-labial (*MMLN*) from the suboesophageal ganglion. Just behind the root of this nerve the sac of the imaginal disc of the prothoracic leg (*T1LD*) is attached to the ventral ganglionic mass and immediately posterior to this point of attachment emerges the prothoracic nerve (*T1N*). Next to it lies the mesothoracic nerve (*T2N*), at the root of which the sac of the mesothoracic leg disc (*T2LD*) is attached to the ganglion. Thereafter there emerge at intervals, from the side of the ventral ganglion, the metathoracic nerve (*T3N*) and

the eight abdominal nerves (*A*1–*A*8). Tracheae enter the ganglia alongside each of the thoracic and abdominal nerves except those of the eighth abdominal ganglion. Another nerve emerges from the ventral ganglion from a point above and behind the root of the prothoracic nerve. This is found to innervate muscles of the prothorax and to anastomose with the prothoracic nerve. Ludwig's interpretation of this nerve as an accessory prothoracic nerve (*APtN*) is therefore accepted. In addition to the lateral nerves of the ventral ganglia, dorsal accessory nerves have their origin in the mid-dorsal line of the ventral ganglion. According to Hewitt, *M. domestica* possesses a pair and three unpaired median nerves in this position. The illustration given by Ludwig seems to indicate three single nerves in this position in *C. erythrocephala*. In *L. caesar* the first pair, which can be referred to as the "median abdominal nerves", are, from their point of origin on the surface of the ganglion, separate. These nerves (*MA*1) serve the first abdominal segment. Behind their origin arise, in turn, the other six pairs of median nerves (*MA*2–*MA*7). The two nerves of each pair are fused for part of their length, the second abdominal pair separating soon after they leave the ganglion, the third at some distance behind the ganglion and the others at successively greater distances from their source. The median nerves of abdominal segments 4, 5, 6 and 7 are much thinner than those of segments 1, 2 and 3 and it is probably because of this that they have hitherto escaped notice. It is interesting to note that there are no median nerves of the thoracic segments but such nerves are represented by three mushroom-shaped bodies attached to the dorsa of the three thoracic ganglia and lying at the loci from which median nerves should arise. The fact that they can be seen, in serial sections, to receive axons indicates that these are vestiges of thoracic median nerves.

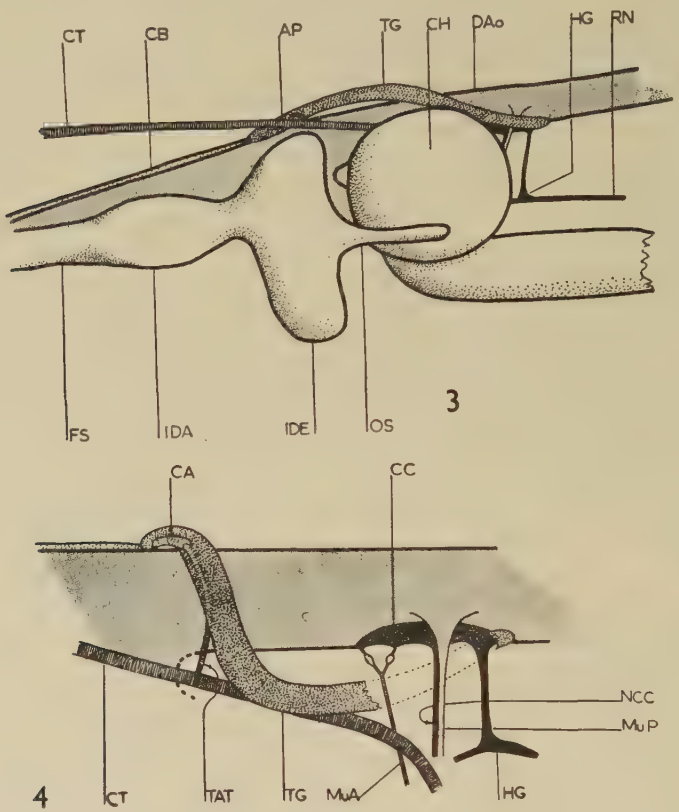
V. The Stomato-gastric Nervous System in *L. caesar*

The frontal ganglion lies above the pharynx, concealed by the muscles of the bucco-pharyngeal apparatus. The single nerve running forward from the frontal ganglion and giving off rami to the cibarial muscles has been identified by Ludwig as the procurrent nerve (*PN*). Nerves unite the frontal ganglion to either labral nerve. The single nerve running posteriorly from the frontal ganglion, and lying above the oesophagus, terminates in the proventricular ganglion, from which rami are given off to the muscles of the proventriculus. This is the recurrent nerve (*RN*), in the course of which there are two ganglia. The first of these is attached to the upper surface of the oesophagus near the point where the crop branches off and from this ganglion (*CG*) go fine nerves to the muscles of the oesophagus and crop. The second is represented by a swelling in the recurrent nerve just behind the brain. From this swelling branches the nerve to the corpus cardiacum and it is, therefore, identifiable as the hypocerebral ganglion.

VI. Weismann's Ring and Related Organs

A detailed description of the anatomy of the retrocerebral endocrine complex in the larva of the Cyclorrhaphan *Protophormia terrae-novae* R.-D. has recently been given by Fraser (1957*b*). In *L. caesar* (figs. 3 and 4) the corpus cardiacum (*CC*) is, as in *P. terrae-novae*, fused with the ventral wall of the aorta (*DAo*).

It receives at its posterior end the nerve from the hypocerebral ganglion (*HG*) and, just in front of this junction, the two nerves from the brain (*NCC*). These issue from the posterior inner faces of the cerebral hemispheres just in front of the points of entry of the cerebral tracheae. There are two muscle strands running alongside the nerves from the brain to the corpus cardiacum (*MuP*). When these muscles diverge from the nerves they pass upwards through the



Figs. 3–4.—*Lucilia caesar* L., larva: (3) lateral view of brain and adjacent organs; (4) diagram illustrating, in lateral view, the location of the retrocerebral endocrine organs. (*CT*, cerebral trachea; *CA*, corpus allatum; for other lettering see text).

ring to join the lateral wall of the aorta. Two similar muscle strands link the anterior end of the corpus cardiacum with the cerebral commissure (*MuA*). There are also two muscle strands, arising from the same points as the two posterior muscle connectives to the aorta, which pass through the cerebral foramen parallel to the recurrent nerve and terminate at the junction of the frontal sac and pharynx.

The thoracic glands (*TG*) in *L. caesar* form a complete ring around the aorta. They unite ventrally and join the aorta just behind the posterior limit of the corpus cardiacum. Dorsally they join above the aorta and form a single

anterior prolongation (*AP*) which is attached to the cephalopharyngeal band (*CB*). The corpus allatum, which is fused to the underside of the prolongation, is globular and not crescentic, as in *P. terrae-novae*. The transverse anastomosing trachea (*TAT*), linking the two cerebral tracheae, passes over the aorta and under the corpus allatum and appears to be fused to both these organs. There are no tracheae penetrating the thoracic glands. The lateral parts of the ring formed by these glands lie on top of the cerebral tracheae and are fused with them at points of contact. Thus the ring in *L. caesar* is a more compact structure with a higher degree of fusion of the components than in *P. terrae-novae*.

Other species examined include *Lucilia sericata* Mg., *C. erythrocephala*, *C. vomitoria*, *M. domestica*, *Muscina pabulorum* Fal. and *Cynomyia mortuorum* L. The structure of the ring and the arrangement of the nerves, connective muscle strands and tracheae in these species resemble so closely those in *L. caesar* that separate descriptions are not warranted. Histological details are similar in the seven other species to those in *P. terrae-novae*. The " chromophile " corpus cardiacum cells, their cytoplasm faintly blue in the living organ and having a strong affinity for methylene blue when supravitally stained, form two parallel lines in the floor of the aorta, representing the two corpora cardiaca now fused. Similar cells also occur embedded in each thoracic gland.

Neurosecretory cells are visible in the living brains of these larvae during the prepupal phase provided, in the case of larvae of *Lucilia* spp., that the specimen is not in diapause. The locations and characteristics of the six neurosecretory cell groups in the brain of the larva of *L. caesar* have been described by Fraser (1957*a*). The cells identified by him as belonging to Group 4 are the ones most easily seen lying in the dorsum of each hemisphere. Their characteristic bluish colour is caused by the presence within them of particulate material which is a neurosecretory product. " Chromophile " cells in the corpus cardiacum may also have a distinct blue colour in life but a particulate product of these cells has not yet been detected by available techniques.

This anatomical study was carried out as a preliminary to investigations of the endocrine control of development, the endocrinology of diapause and the neurosecretory centres controlling endocrine activity in *L. caesar*.

VII. Acknowledgments

This work was carried out while I was in receipt of a grant from the Agricultural Research Council. I wish to thank Dr. A. R. Hill and Mr. D. G. Cochrane for helpful criticism and Mr. W. Smith for his assistance in maintaining the insect cultures.

VIII. Summary

The anatomy of the central nervous system, and distribution of nerves from it, in the larva of *Lucilia caesar* L. are described and the occurrence of median abdominal nerves, hitherto unrecorded, is noted. A detailed account of the stomato-gastric nervous system and of Weismann's ring and related organs is given, with a brief comment on the anatomical concordance in larvae of six other species of Cyclorrhapha. The unique anatomical arrangement of these

organs in *Protophormia terrae-novae* R.-D. is emphasised. The location and appearance of neurosecretory cells in the living brain are discussed.

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CORRECTION.

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In the original Notice of the above work (*antea*, p. 140) the name of the English agent was unfortunately omitted ; the complete details are given above.

INDEX

ERRATA

p. 45, line 16. For " *Phloephthorus* " read " *Phloeophthorus* "
p. 88, couplet 1. For " *Beraea odesminuta* " read " *Beraeaodes minuta* "